SOME UPPER CRETACEOUS AND EOCENE FRUITS FROM EGYPT

BY

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SOME UPPER CRETACEOUS AND EOCENE FRUITS FROM EGYPT

By M. E. J. CHANDLER

SYNOPSIS

The occurrence and preservation of fruits and seeds from the Dano-Montian and Eocene of Egypt is described, and previous work summarized and in some instances revised.

These Egyptian fossils are clearly related to the London Clay Eocene plants on the one hand and to the Recent flora of South-Eastern Asia on the other as shown by the occurrence of *Nipa* in all three floras. The historical and geographical connexion of the three floras is considered, due attention being paid to recent work on plant migration by Chaney and Axelrod. The conclusion is reached that whereas all Tethyan (Indo-Malayan) types of flora may have their remote origin in a uniform palaeotropical plant belt in Early or Middle Cretaceous times, some secondary centre of colonization must be postulated for the Eocene tropical flora of Western Europe where the original palaeotropical angiosperm flora must have been exterminated by the Cenomanian transgression.

The obvious source of recolonization lay in South-Eastern Asia, because the great East–West Tethyan ocean must have constituted a formidable barrier to mass migration from the African continent. Moreover the marked Malayan relationship of the London Clay flora supports its immediate Asiatic origin. Detailed systematic descriptions of the Egyptian fruits are given.

INTRODUCTION

A few fossil fruits recently discovered in Egypt were sent to the British Museum for identification. They are of great importance, for hitherto the bulk of our knowledge of the ancient flora of North Africa has been derived from the study of wood (Kräusel, 1939), whereas fruits and seeds were almost unknown. The majority of the specimens came from the Dano-Montian Lower Esna Shales between latitudes 25° and 27° N. They were collected by two Egyptian geologists, Doctors M. Y. Hassan and M. I. Youssef, who in appendices to this paper give details of the deposits which yielded the fruits. (See also note on p. 187).

Dr. Hassan's finds were from the Kharga Oasis of the Western Desert, Dr. Youssef's from the Kosseir area bordering the Red Sea.

Like the London Clay, with which comparison will be made in the following pages, these plants occur in marine beds with a marine fauna, and must be presumed to have been derived from the nearby land surface of the African continent a little further south.

By a curious coincidence a fruit from the Lutetian (or possibly slightly younger beds of Eocene age) of Egypt was also received for study at about the same time. It was collected by members of the Anglo-Egyptian Oil Company, Messrs. Thiébaud and Robson, at Wadi Rayan in the Western Desert, i.e., at about latitude 29° N. in the Fayum. It is an extremely puzzling specimen, and some points about its anatomy are rather obscure.

The preservation of these fruits and seeds is interesting and somewhat variable. Some of them, e.g., *Palaeowetherellia*, are reproduced cell by cell in limonite in part at least. Indeed they display the details of their structure almost as well as the pyritized fruits of the London Clay. They have the merit of being more stable and permanent in their preservation than pyritized specimens, but this advantage carries with it the disadvantage that they do not so readily disintegrate and fall to pieces along structural lines and natural planes of weakness as the London Clay pyritized fossils so frequently do. Some of the best and most delicate evidence from the London Clay fruits came from decaying specimens, not from those which were artificially sectioned.

But some of the Egyptian fossils, e.g., Icacinaceae, have the appearance of being purely internal casts, for although they were already chipped, no cell-structure was exposed, or if visible was so indurated as to show little detail. Such specimens are unlikely to provide more information if broken or sectioned, and it therefore seems pointless to sacrifice them where clear and unmistakable evidence of internal structure along natural planes of weakness is lacking. It is highly probable that future collectors will in due course supplement the present meagre evidence from such tantalizing casts.

Several of the new Dano-Montian specimens agree with one (V.12985) which has been in the collection at the British Museum (Natural History) since 1912. This was described by Kräusel (1939 : 106, pl. 2, figs. 9, 10 ; text-fig. 32) and was referred by him to *Diospyros schweinfurthi* Heer. It came from the Lower Danian of Farafra in the Western Desert at latitude 27° N. approximately. Heer's supposed *Diospyros* and another specimen which he named *Royena desertorum* were originally described by him in 1876 (see p. 168).

The examination of the new material, and more especially of a newly fractured surface of V.12985, leaves no doubt that Heer's "*Diospyros*" and "*Royena*" both belong to a single species which has no connection with the Ebenaceae. The species, named hereafter *Palaeowetherellia schweinfurthi* (Heer), is obviously closely related to *Wetherellia variabilis* Bowerbank from the London Clay, and to another species *W. dixoni* (Carruthers)—to be redescribed—from the Bracklesham Beds of Selsey. The genus is now referred tentatively to the family Euphorbiaceae.

Apart from the above, only six Tertiary angiosperm fruits from Egypt have previously been recorded :

Palmacites rimosus Heer from the Danian of Kharga (Heer, 1876 : 11, pl. 1, figs. 21, 22), an imperfect fruit of which no really distinctive characteristics are shown or described. The anastomosing "fibres" in fig. 22 may be nothing more than compression ridges such as are seen in places on the fruit of *Icacinicarya youssefi*. Heer's determination must be regarded as very doubtful pending re-examination of the specimen.

Securidaca tertiaria Engelhardt (1907 : 213, pl. 19, fig. 6) from the Eocene of the Fayum. It would be unwise to comment upon this aceriform fossil without the most careful scrutiny of the original material combined with a comprehensive study of living fruits of this type in the various families in which they occur.

Nipadites sickenbergeri Bonnet from the Middle Eocene Nummulitic Limestone

(Marine Lower Mokattam of Gebel Giuchi, Mokattam), a species which the available evidence identifies with *Nipa burtini* (Brongniart) (see pp. 159, 162).

Rubiaceocarpum markgrafi Kräusel from the same beds which is clearly the same *Nipa* represented by seeds with outer integument preserved (see pp. 161, 163).

Nymphaeopsis bachmanni Kräusel from the Lower Oligocene of Cairo (Kräusel, 1939 : 39, pl. 2, figs. 2–8 ; pl. 3, fig. 8 ; pl. 21, fig. 6 ; text-fig. 7) has features which suggest that puzzling material has been wrongly interpreted. Further reference is made to the matter on p. 183 when the structure of *Thiebaudia rayaniensis* is discussed.

Teichosperma spadiciflorum Renner (1907 : 217 ; Kräusel & Stromer, 1924 : 33, pl. 1, fig. 2 ; text-figs. 1–3) from the Lower Oligocene of the Fayum, referred tentatively by Renner and with more certainty by Kräusel & Stromer to Pandanaceae, needs re-investigation especially as regards the number of locules and form of the seed. If the seed is really curved as Kräusel & Stromer's text-fig. 3 shows, the family Myrtaceae should be explored. But before making confident statements about this, it might be necessary to examine serial sections. Without further evidence no really satisfactory determination can be made, although relationship to Pandanaceae seems highly improbable.

It is not surprising that fruits from a remoter period of angiosperm history than the Tertiary material hitherto studied are difficult to relate to living genera or to place in Recent plant families. But in spite of the fact that it has not been possible to identify all the specimens, the interest and significance of this tiny flora are out of all proportion to its size.

The list of the newly found plants is given below.

		Horizon and locality		
Family	Genus and species	Lower Danian	Dano-Montian	Lutetian (approx.)
Nipaceae	*Nipa burtini* (Brongn.)	—	Kosseir	—
Anonaceae	*Anonaspermum aegypticum* n. sp.	—	,,	—
Euphorbiaceae	*Lagenoidea trilocularis* Reid & Chandler	—	,,	—
	Lagenoidea bilocularis Reid & Chandler	—	,,	—
Euphorbiaceae ?	*Palaeowetherellia schweinfurthi* (Heer)	Farafra	Kharga and Kosseir	—
Icacinaceae	*Icacinicarya youssefi* n. sp.	—	Kosseir	—
	Icacinicarya sp. ?	—	,,	—
Flacourtiaceae ?	*Thiebaudia rayaniensis* n. gen. et sp.	—	—	Wadi Rayan
Incertae sedis	*Carpolithus hassani* n. sp.	—	Kharga	—
	Carpolithus sp. (*Icacinicarya* ?)	—	,,	—
	Carpolithus sp.	—	Kosseir	—

Fuller details of localities are given under the descriptions of the species in the systematic part of this paper. No attempt has been made to determine a few small twigs.

These discoveries are of outstanding importance for a number of reasons :

(1) As stated above, fossil fruits and seeds of any age are rare in Egypt. The recent finds suggest that careful collecting, persisted in over a long period, would reveal the presence of a considerable flora in that region.

(2) Very little is known about pre-Tertiary angiosperm fruits and seeds from any area whatsoever. Knowledge derived from leaves or wood is usually complementary to that based on fruits and seeds rather than strictly comparable with it. This was discussed by Reid & Chandler (1926 : 10–13). Plant organs such as leaves tend to be preserved in different deposits from fruits and seeds and to represent different elements in the parent plant-formations. But here in Egypt are data from pre-Tertiary Beds which are really comparable with the abundant Tertiary records of fruiting organs elsewhere.

(3) The plants from Egypt are quite obviously related to the Tethyan type of flora found in the London Clay. For even in so small a group as this under discussion similar or identical genera and even species occur. Note the presence of *Palaeowetherellia* (a distinct genus and species representing *Wetherellia*), of a *Nipa*, of the two species of *Lagenoidea* actually found in the London Clay (so far as present information can demonstrate), of an *Anonaspermum*, and of the family Icacinaceae. Here is impressive evidence that the Malayan type of flora so characteristic of the London Clay was already present in Africa towards the end of Cretaceous times. It must be presumed to have flourished on the southern sea-board of the ancient Tethys ocean.

(4) The presence in Egypt of a flora of strong tropical Malayan affinity, for such must be the relationship of any flora at all comparable with that of the London Clay, confirms the view supported by other lines of evidence that the climate of Africa to the north of the equatorial belt must have been remarkably different during the late Cretaceous and Eocene from what it is today. *Nipa* and its associates demand not only warmth but a high degree of humidity (Reid & Chandler, 1933 : 74 *et seq.*).

The discovery of this Tethyan flora in Egypt at the end of the Cretaceous must inevitably raise the question, " What was its historical and geographical connection with the biologically similar floras in the London Clay in Eocene times and in Indo-Malaya at the present day?"

Did the Egyptian flora with the characteristic *Nipa* and its associates arise in remote times in South-East Asia and spread thence into the African and European continents as climatic conditions, combined with available migration routes, favoured its expansion, or had it some other origin ? From what primitive source or sources were these three related floras derived ?

Professor Kryshtofovich expressed the opinion that in the tropics of South-East Asia the Malayan type of flora had remained " unmolested ever since its first descent from its Cretaceous ancestors " (1929 : 310, 311).

Reid & Chandler (1933 : 82) stated that in their opinion the London Clay flora had its origin in Malaya, whence it migrated northwards and westwards along the shores of the Tethys ocean to Western Europe.

The late Professor Seward criticized the views of these three authors on the grounds that the early Tertiary flora of South-East Asia is but little known, and that the evidence concerning it, if it exists at all, has not yet been published (1934 : 23), so that there may, for all we know, have been no Tethyan type of flora in Indo-Malaya in the early Tertiary which could have served as a centre of dispersal.

He propounded two alternative suggestions as to the origin of the Tethyan flora in Europe :

(1) That like the later Tertiary floras it may have reached Europe " not from a South-Eastern home but from the North."

(2) That the London Clay flora may have been part of a widespread flora " which in the course of the Tertiary period suffered progressive reduction and is now represented by enfeebled relicts in Indo-Malaya."

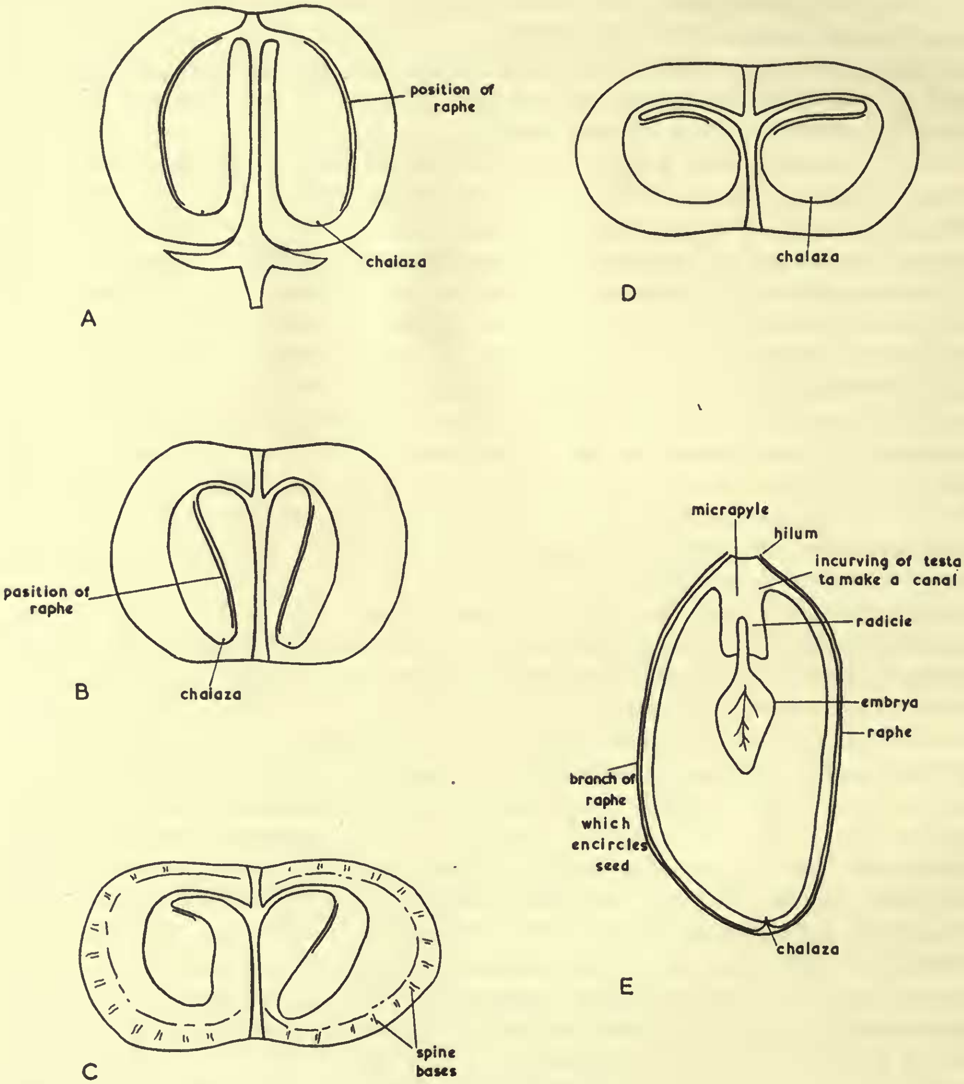
Before discussing these suggestions it may be of value to digress so as to take account of recent important American contributions to plant history set forth by Professor Chaney in two papers (1940, 1947). Chaney bases his views on successive American fossil floras. These show that there was gradual displacement of temperate to warm-temperate Cretaceous forests in low and middle latitudes in the United States at the end of the Cretaceous period. Their place was taken by warm temperate to sub-tropical vegetation (the Neotropical flora of Chaney) of Lower Eocene age derived largely from the Antillean region on the East, and from Mexico and Central America on the West. Evidently, he states, an early Tertiary *northward* movement of plant populations as a whole occurred, so that the temperate forest type of vegetation became concentrated in high latitudes, while tropical and subtropical vegetation, now characteristic of forests near the Equator, spread into middle latitudes, reaching 50° N. approximately on the western side of the continent, and 37° N. on the eastern side.

Professor Chaney compares American plant history with that of the Old World, and emphasizes that in approximately the same period a parallel story of plant migration occurs there, modified to some extent by the extensive East-West barrier of the Tethys ocean, which caused some differentiation of vegetation to the North and South of it in Eocene and later times. He makes special mention of the tropical Malayan London Clay flora at latitude 50° N. on the west side of the Eurasian continent whose modern equivalents (notably *Nipa* and mangrove) grow in the rain-forest of Indo-Malaya. He also lists and shows on a map (1940 : 482, 483, text-fig. 1) numerous Eocene and a few Oligocene (palaeotropical) floras of the Old World which have similar tropical relationship, while localities for the corresponding (neotropical) floras in the New World are also plotted. He then recalls that since the Oligocene a reverse movement has taken place in both hemispheres, the subtropical and tropical forests gradually moving south again, giving way both in North America and in Eurasia to that temperate vegetation which he calls the Arcto-Tertiary flora.

In America the tropical vegetation has survived in the Antilles, the North of South America, Central America and Mexico, with a few remains in South Florida. In Eurasia it survives in south-east Asia.

Chaney perceives that such a wide-spread shifting of forest distribution must be due to factors which were world-wide in operation, affecting whole plant populations

(1947 : 141). If, as appears from the evidence available, he is right that migration from the end of the Cretaceous onwards to the Oligocene was northwards, so that plants from equatorial regions extended into middle latitudes, then the suggestion made by Seward that the Eocene tropical floras, like the later ones, may have reached Europe from the North does not fit into the picture and cannot be seriously enter-



Text-fig. 1. A–D Longitudinal sections through fruits showing placentation (diagrammatic). A. *Diospyros* sp. Recent. B. *Wetherellia variabilis* Bowerbank. London Clay; Sheppey. C. *Wetherellia dixoni* (Carruthers). Cuisian ?; Selsey. D *Palaeowetherellia schweinfurthi* (Heer). Upper Cretaceous; Egypt. E. Longitudinal section through seed, *Diospyros* sp. Recent.

tained. There is certainly no evidence in Europe of a Malayan flora in more northerly stations than the London Basin.

Reid & Chandler (1933 : 62) were convinced by its past distribution and present physiological requirements that the *Nipa* flora in the London Clay was living at the most northerly limit of the climatic conditions (both of temperature and humidity) which it could tolerate. Hence it is improbable that it could have come into being in yet more northerly regions which would have been still more unfavourable in these respects, regions which were, moreover, already occupied by the Arcto-Tertiary type of vegetation suited to them. For these reasons the origin of the Malayan flora to the North appears to be untenable.

Before considering Seward's other alternative suggestion, it may be helpful to summarize briefly the facts (and deductions from them) which should be borne in mind and correlated in any further consideration of these problems. They are as follows :

(1) A late Cretaceous Tethyan flora in Egypt found at approximately 25° to 30° N. probably derived from the African mainland at no great distance to the South.

(2) An early Eocene Tethyan flora in Western Europe extending North to latitude 50° approximately.

(3) The presence of similar tropical or sub-tropical floras in the Eocene and Oligocene situated apparently along the former northern boundaries of the Tethys ocean, as many of these floras yield *Nipa*.

(4) A living Tethyan type of flora restricted to South-East Asia (the Indo-Malayan flora).

(5) A northward extension of the equatorial tropical forest belt between Cretaceous and Oligocene times coinciding with the broadened latitudinal belt of increased temperature and humidity.

With these facts and deductions in mind, we now turn to Seward's second alternative theory, viz., that the Tethyan flora was part of a widespread flora which suffered progressive reduction, surviving in Indo-Malaya today. This is an unquestionably true statement, for on actual fossil evidence, so far as it goes, the flora of Indo-Malaya, or something closely akin to it, was once much more widely distributed (Chaney, 1940 : 482–485, text-figs. 1, 2 ; Edwards, 1936 : 28, text-fig. 9, map showing the distribution of *Nipa* in relation to the approximate outlines of the Tethys ocean). But Seward's statement does not carry the matter far enough ; it requires much more elucidation. Nor does it exclude the possibility of an *immediate* (early Eocene and post-Cretaceous) Malayan origin for the palaeotropical vegetation of Europe.

In support of the theory that the various Tethyan floras originated within a uniform tropical belt of vegetation reference may be made to Axelrod (1952). He believes that in the Lower Cretaceous, "long distance migration may have been more effective than at any later time," producing a more or less uniform type of vegetation within given climatic belts.

During that period, he points out, the angiosperms were beginning to compete successfully with the older waning Mesozoic floras which they were in process of supplanting. He visualizes that by Middle Cretaceous times there must have been basic, more or less world-wide, angiosperm floras with the minimum of regional differentiation, viz., a tropical to sub-tropical flora in lower and middle latitudes more uniform in type throughout the world than has existed at any time since that period, and a uniform temperate flora at higher latitudes.

It is not unreasonable to suggest that Axelrod's uniform tropical angiosperm flora was the source from which the Recent tropical flora of South-East Asia and the Cretaceous-Oligocene tropical flora of North Africa were derived by direct and unbroken descent within these two regions. It may also have been the source of the Eocene European tropical flora, not by direct descent in Western Europe but by a more circuitous route. These suggestions are considered and explained in greater detail below.

There is no reason to think that in Equatorial Asia there was ever a period during the Tertiary when tropical conditions did not persist. Therefore it is not unreasonable to postulate that the old palaeotropical flora probably survived over the equatorial belt in that part of the world throughout Tertiary times, even after the Oligocene, when it was driven south of its maximum Eocene extension. In that equatorial belt it would have retained or gradually evolved a character of its own, viz., that of the Indo-Malayan flora as we know it today. This is essentially the opinion expressed by Kryshtofovich and quoted on p. 152.

In Africa the course of events may have been somewhat similar. Following upon the contraction of the Tethys sea in Oligocene and later times and the resulting climatic changes, the Tethyan flora must have been driven from the more northerly part of its former Cretaceous and Eocene territory by the pressure of unfavourable conditions. But it could probably have survived in the tropics of Central Africa. Desiccation combined with the southern trend of plant migration in post-Oligocene times would undoubtedly have prevented any later return to the more northerly latitudes it had previously occupied. Deserts and the Tethyan sea (or its shrunken remains) would probably have cut it off effectively from Asia. But within the African equatorial belt it may have persisted, possibly giving rise (or giving place ?) eventually to a distinctive African tropical vegetation as it evolved in isolation from the Asiatic stream of life.

But what of the London Clay Eocene flora of Britain, and how was it related to the uniform palaeotropical flora of Lower Cretaceous times ?

There can be no doubt that the Lower Cretaceous flora of this country must have been eliminated by the great marine transgression of the Upper Cretaceous. This transgression far overpassed the most northerly limits of tropical climate for which there is any evidence, viz., about latitude 50° N. If the European Lower Cretaceous palaeotropical flora persisted at all it must have been on islands, or on tracts of land on the western borders of the present European continent, perhaps on land margins now submerged beneath the sea. If Chaney is right about the world-wide character of climatic changes, the flora could not, in all probability, have survived unless land nearer the Equator was accessible for colonization during the late Cretaceous. For in America, as we have seen, temperate and warm-temperate forests occupied low and middle latitudes at this period, from which latitudes they were driven only at the end of the Cretaceous by the northward march of Equatorial vegetation. It seems obvious that with the withdrawal of the Upper Cretaceous sea the re-exposed land surface (now having a sub-tropical or tropical climate) would have been available for recolonization by a flora of tropical type. This may have come either from southern and western plant " reserves " as suggested above, or from the only two alternative sources, viz., the African continent, or the south-east of Asia. In the former we know that a Tethyan flora was present in the late Cretaceous. In the latter there is no reason to doubt the existence of such a flora at that time as has been pointed out above.

The theory of recolonization from the west offers no adequate explanation of the marked Indo-Malayan aspect of the incoming Eocene flora. It is unlikely that closely parallel development would have taken place independently in two such widely separated areas. It is equally improbable that the source of recolonization was the African continent. Had no serious physical barrier existed, the natural solution of the problem would be to assume that by Eocene times the Cretaceous Tethyan flora of Africa had migrated northwards and spread into Europe, as it followed the extension in latitude of the hot and humid climatic belt favourable to it.

But the existence of the great ocean barrier of the Tethys over perhaps 1,000 miles or more from South to North must have had a marked deterrent effect.

Axelrod (1952) discusses conditions affecting the migration of faunas and floras in geological times. He maintains that plant distribution at any particular time is " largely a reflection of the climates available for occupancy " (p. 177), i.e., climate is the chief factor controlling plant migration. But whereas he considers that a much higher degree of probability exists for plants than for animals in the matter of over-water dispersal, he is also sure that " within any given climatic region distance will finally impose a barrier to the migration of plants also." It is only fair to him to state that in spite of this, he regarded the presence of palaeotropical Tertiary vegetation on both sides of the Tethys as evidence that the sea in this particular case (as well as in others) did not prevent the distribution of the flora on both sides of it (1952 : 187). But this is a curious conclusion to have drawn, for he also explains that " The water barrier that a continental flora can transgress within an epoch of time (say, 10 to 15 million years) is not unlimited," while beyond 200 to 250 miles the probability of colonization by a whole flora is low. Hence what he designates the " waif assemblages " of ocean islands which lack balance, since whole classes and orders expected are absent, while others are only poorly represented. " It would appear," Axelrod writes, " that long-distance, over-water migration has not been generally effective in populating widely separated continents." Even during much longer periods of time, therefore, there may be good reason to doubt whether the Tethyan flora in Africa could have migrated directly across the great ocean which lay athwart its path to the North. Further, as Reid & Chandler (1933) pointed out, the London Clay flora shows far less affinity with the flora of Africa than with that of South-East Asia.

To the present writer, therefore, it seems highly improbable that wholesale migration took place across the Tethys.

There remains the third suggested source for the post-Cretaceous colonization of

West Europe, namely the South-East Asiatic. On such evidence as is available this appears to be by far the most probable source for these reasons :

(*a*) The Indo-Malayan region and Southern England both lay within the palaeotropical climatic belt of Eocene times.

(*b*) The northern shores of the Tethys and the land adjoining were so situated as to provide a possible migration route from South-East Asia to West Europe within this greatly extended tropical belt of Eocene times which allowed the flora of equatorial regions to occupy many degrees of latitude North of its present limits.

(*c*) The London Clay flora is more closely linked with that of Indo-Malaya than with that of any other existing flora.

The final answer to these speculations can only be provided by extensive research on fossil floras from many widespread regions. At present the evidence is insufficient to furnish incontrovertible proof, but the balance of probability seems in favour of a remote origin of the Tethyan type of flora within a uniform palaeotropical belt in the early Cretaceous, and of an immediate origin of the London Clay flora by migration from Indo-Malaya between Cretaceous and early Eocene times.

The subsequent history of the London Clay flora and the reasons why it survived only in Indo-Malaya have been set forth by C. & E. M. Reid (1915), Reid & Chandler (1933), Chaney (1940, 1947) and others. When during the Oligocene the connection of the Tethys with the Indian Ocean was broken so that the former vast waterway became a huge land-locked Mediterranean, while the great transcontinental mountain barriers of Eurasia were being uplifted, progressive cooling of the climate in middle latitudes occurred, so that more temperate plants from the North gradually supplanted the former tropical ones of the Eocene. During this period final extermination was the fate of the Tethyan flora in Europe. With the shrinking of the Tethys a migration route to Asia no longer existed under favourable climatic conditions. The direct route to the tropics in the South was blocked by the combined barriers of East–West mountains and the East–West remains of the Tethys, as effectively as Northward migration had formerly been blocked by the vaster Tethyan ocean of late Cretaceous and Eocene times.

But in South-East Asia, as already stated, survival of the palaeotropical flora and its descendants was possible, for there is no reason to think that equatorial latitudes in that continent have ever passed through a phase when it could not have retained its tropical flora. Even when the more northerly parts of the palaeotropical belt became cooler, so that the tropical flora could no longer live in them, migration to more southerly regions was possible, thanks to the absence of East–West barriers and to the existence of North–South valleys and coastal plains.

Meanwhile it is likely that the Tethyan flora of Egypt, when more fully known, will reveal a far stronger African element than is found in the London Clay, cut off as this latter appears to have been from direct communication with the African continent throughout its history.

The affinities of unknown plants in the Egyptian fossil flora should therefore be sought among tropical and sub-tropical African genera of the present day as well as among those of South East Asia.

I wish to express my warmest thanks to Mr. W. N. Edwards for helpful suggestions and criticisms, and to Mr. F. M. Wonnacott of the Geological Department for much help in the preparation of the manuscript for the press.

SYSTEMATIC DESCRIPTIONS

Note.—The specimens, with two exceptions, are from the Dano-Montian Lower Esna Shales of Egypt.

Those from Kosseir Area, Red Sea, were collected by Dr. M. I. Youssef, those from Kharga Oasis by Dr. M. Y. Hassan, to both of whom I am indebted for the opportunity to study these most interesting plants and for the generous gift to the British Museum of the figured specimens.

The other two horizons and localities represented are the Lower Danian of Farafra (*Palaeowetherellia*), and the Eocene beds of Wadi Rayan (*Thiebaudia rayaniensis* gen. et sp. nov.).

MONOCOTYLEDONES

Family NIPACEAE

Genus ***NIPA*** Thunberg 1782

Nipa burtini (Brongniart)

(Pl. 10, figs. 1–5 ; pl. 11, figs. 7–9)

1904. *Nipadites sickenbergeri* Bonnet, p. 499, figs. on pp. 500, 501.
1924. *Nipadites sickenbergeri* Bonnet : Kräusel, p. 36.
1939. *Nipadites sickenbergeri* Bonnet : Kräusel, p. 22, pl. 1, figs. 1–18, text-fig. 1.
1939. *Rubiaceocarpum markgrafi* Kräusel, p. 108, pl. 1, figs. 19–24.

For full synonymy see Reid & Chandler (1933 : 118).

LOCALITIES AND HORIZONS. North slopes of Mokattam, near Cairo ; Middle Eocene. Gebel Atshan, Kosseir Area, Red Sea ; Dano-Montian Lower Esna Shales.

DESCRIPTION AND REMARKS. The discovery of a small *Nipa* fruit in the Dano-Montian of Kosseir and the re-investigation of fruits named *Rubiaceocarpum markgrafi* Kräusel from the Middle Eocene of Mokattam made it necessary to re-study *Nipadites sickenbergeri* Bonnet from the same beds as *Rubiaceocarpum*.

As a result it can be stated with confidence that *Rubiaceocarpum* is a *Nipa* seed with outer integument preserved in part at least, and that it, and the seeds named *Nipadites sickenbergeri*, cannot be separated from *Nipa burtini* (Brongn.) in the present state of our knowledge.

This conclusion was forced by the evidence upon the writer who had started with the conviction that *N. sickenbergeri* was distinguished beyond question from *Nipa burtini* by its ribbed and furrowed seed. Moreover the opinion expressed by Reid & Chandler (1933 : 122) that the fossils should be referred to *Nipa* rather than to *Nipadites* is now re-affirmed.

In order the better to understand the fossils a further examination of the living *Nipa fruticans* was carried out. The following details may now be added to those recorded by Reid & Chandler (1933 : 122).

The hard compact endocarp when freed from the adherent pericarp (or sarcocarp) is more or less smooth but shows on its outer surface, in the parenchyma which covers it, impressions of stout longitudinal fibres. There is no conspicuous fluting or ribbing of this surface, but a tangled mass of finer fibres can be seen where the parenchyma is rubbed off. When abrasion is carried a stage further stout transverse fibres are exposed. These were observed in 1933. The locule shows conspicuous flattened transverse or oblique fibres and stout longitudinal ones overlying them which readily break away.

When an endocarp is cut transversely, a nut-like seed may fall free if the material is in a suitable state of preservation. This bears upon its surface conspicuous flutings due to narrow deep furrows in a parenchymatous layer. In the furrows there are remains of fibres which probably belong to the endocarp. They have usually been torn away, leaving empty furrows only on the surface of the seed. Some of the fibres branch or unite so that the furrows and intervening ridges are not aways absolutely straight and longitudinal, although this is their general alignment. On the flat or slightly convex broad ridges between the furrows can be seen impressions of the transverse or oblique flattened fibres which belong to the locule wall described above (Pl. 11, fig. 10).

In Reid & Chandler's description this coat of the testa was regarded as part of the endocarp because endocarp and testa are often fused. On the detached seed there is a deep narrow parallel-sided furrow (Pl. 11, fig. 12). This is formed by an incomplete longitudinal ridge or septum which projects into the locule from the whole length of the carpel wall. The large sub-circular or circular basal aperture giving access to a cavity in the endosperm is a conspicuous feature also, and is associated with the embryo. The outer pulpy integument of the testa is fairly easily scraped away, exposing a close-textured rather brittle, gummy or resinous inner integument with a smooth transversely striate outer surface of fine cells. Embedded in the surface of this coat are a few flat fibres which branch and anastomose to form a coarse network. The fibres lie obliquely, transversely, or more infrequently longitudinally (Pl. 10, fig. 6). On the inner side of the brittle inner integument is a raised network due to very fine fibres so arranged as to form fine transversely elongate meshes.

The inner integument follows fairly closely the contours of the endosperm, but is separated from it by a thin soft film of fine cells. When the endosperm has rotted, as may happen in specimens which have drifted in the sea for some time, the empty integuments of the seed may still remain attached firmly to the endocarp as it lies within the drupe, but the film of cells just described has usually gone so that only the network of fibres with transverse meshes covers the exposed surface. It is the internal cast of this coat with its fibres which shows the ornamentation described on seed-casts of *Nipa burtini* from the London Clay (Reid & Chandler, 1933, pl. 2, fig. 6).

No raphe or chalaza scar is visible on the interior of the inner integument in

Recent fruits, nor is their existence indicated by any change in the alignment of the fine fibrous network so far as I have been able to observe. When all the integuments are removed so that the actual endosperm is uncovered, a series of even finer furrows and ridges, like minute ruminations, are laid bare. At the apex and over the sides of the endosperm their orientation is clearly transverse (Pl. 10, fig. 6 ; Pl. 11, fig. 11). At the base they are coarser and the alignment more irregular, giving rise to small low rounded lobes of endosperm. Whatever the orientation, the small areas which they produce on the surface are more or less convex, especially when slightly weathered or abraded. The endosperm sometimes displays a few broad shallow longitudinal furrows or sinuosities at the lower end which gradually die out above (Pl. 11, fig. 12). They resemble the furrows sometimes seen in *Nipa burtini* and *Nipadites sickenbergeri*. On the exterior of the complete seed they are barely discernible, being obscured by the spongy outer integument. Nor are they usually apparent on the inner surface of the empty testa.

The astute observer Hooker in an editorial note (Le Maout & Decaisne, 1876 : 822) comments that the seeds are erect and anatropous. But for this observation I should not have suspected their anatropous character, for there is no more indication of a raphe on the outer surface of the testa than there is on the inner surface. Nevertheless examination of a detached endosperm-mass supports Hooker's statement, or at least gives evidence of comparable structures. After removal of the integuments a flat band of fibres was seen lying in one of the shallow longitudinal furrows of the surface. It extends upwards from the base almost throughout the length, follows a straight course, and is parallel-sided, quite different in character from the somewhat sinuous flat fibres in other furrows. That this is a definite structural feature, probably the raphe, is confirmed by the differentiation of a band of endosperm immediately beneath it. In this position there are small irregular rounded " ruminations," not transversely elongate ones as elsewhere, and some indication of longitudinal alignment is given by a tendency for longitudinal cracks to form (Pl. 11, fig. 11). Somewhere in this band the fibres must enter the endosperm and pass to the chalaza. But the point of entry is so inconspicuous that it is hidden by the irregularities of the " ruminate " surface. Nevertheless a corresponding structure shows clearly in some fossil material, as will be described later.

From the details given above it is fairly clear that the appearance of a fossil *Nipa* must vary considerably with the coat which happens to have been preserved or exposed. This depends partly on the mode of preservation of the fossil. Thus an internal seed-cast may show the structure of the endosperm as in the Egyptian *Nipa*, or it may merely be a cast of the inner integument formed after the endosperm had decayed as in many London Clay seeds.

Any seed having the ridged outer integument preserved would have the distinctive appearance of *Rubiaceocarpum*, further details of which are given later. In a broken fruit some layer or layers of the endocarp may show, as in many fruits from the London Clay, and in a small Dano-Montian fruit from Egypt. In the London Clay fruits wear and tear has often exposed the inner layers of endocarp with flat transverse fibres described in 1933. By far the most common specimens at Sheppey and Herne Bay are fruits (perfect or imperfect), showing stout fibres embedded in the spongy tissue of the sarcocarp. Rarely is the epicarp preserved, and then only in fruits freshly removed from the matrix. It quickly cracks and falls to pieces on exposure to air.

It seems scarcely necessary to repeat detailed descriptions of the fossil fruits and seeds which have already appeared in published work (Reid & Chandler, 1933 : 119 ; Kräusel, 1939 : 22 ; Seward & Arber, 1903, etc.). Other references will be found in the synonyms listed by Reid & Chandler (1933 : 118).

The question inevitably arises once more, " How many fossil species can be distinguished in the deposits with which we are now concerned ?"

It must be remembered that whereas the London Clay fruits and seeds are relatively uncrushed, the Egyptian ones have often undergone an excessive amount of deformation by crushing and there appear to be no valid and consistent grounds for separating *Nipa burtini* and *Nipadites sickenbergeri* as distinct species. The longitudinal ridging and furrowing of the seed-casts, or its absence, although it was supposed by Bonnet to be of specific value, cannot really be used in diagnosis, for although smooth seed-casts are common in the London Clay, furrowed ones may also occur. Moreover both kinds are found in the Egyptian Eocene (Bowerbank, 1840, pl. 4, fig. 1; pl. 5, fig. 1 ; Kräusel, 1939, pl. 1, figs. 11–13).

Again in the Egyptian casts the furrows may be few and slight (V.13695) or fairly conspicuous, or in some cases, overemphasized by crushing.

The other chief difference which occurs in some cases between fossils from the two localities lies in the size. But differences in size are no more satisfactory than furrowing, as a reason for specific separation. It is true that the majority of *Nipa burtini* fruits and seeds from the London Basin are smaller than the majority of the seeds from Egypt, and that they vary greatly in appearance. Yet large nuts do occur in the London Clay (Bowerbank, 1840, pl. 5, fig. 1), while very large fruits and seeds occur in the Belgian strata (Seward & Arber, 1903). On the other hand the small fruits from the London Clay are indistinguishable from a Dano-Montian fruit from Kosseir (Pl. 10, figs. 1, 2). Perhaps the predominance of small forms in one area and large in another may be due to the sorting effects of specific gravity rather than to systematic differences. The associated fruits of other families at Sheppey and Herne Bay are on the whole fairly small.

The following table shows minimum and maximum sizes of fossil Nipas from previously published records. It must be remembered, however, that a far larger number of specimens are known from the London Clay than from the other deposits and they include many immature or abortive fruits.

London Clay	Belgian Eocene	Egyptian Eocene
Fruits :		
Length, 1 to 18 cm.	7·5 to 21 cm.	Not known
Breadth, 1·3 to 12 cm.	3 to 15 cm.	,,
Seeds :		
Length, 2 to 8·9 cm.	9 to 10 cm. (commonly 8·5 to 9 cm.)	7·5 to 11 cm. (commonly 8·5 or 9 cm.)
Breadth, 1·3 to 7 cm.	9 cm. (commonly about 7 cm.)	3·4 to 12·3 cm. (commonly about 5 to 7 cm.)

Thus whether furrowing or size be considered, there appear to be no sharp lines of demarcation between species from the localities with which we are concerned.

If furrowing and size cannot be used as a basis for separating species—and it is difficult to see how they can when every gradation may occur in these characters—there are no other grounds obvious on which the diagnosis of more than one species can be based.

Certainly the differences between the Nipas from the two areas under review are no greater than the differences among individual specimens in the London Clay itself (cf. Bowerbank, 1840, pl. 4, fig. 1; pl. 5, fig. 1). Yet there is no reason whatsoever for creating more than one species in this deposit.

A few additional observations on the Egyptian nuts may not be out of place here. Kräusel's figured specimens are largely seed-casts and might be expected to show endosperm structure. Unfortunately the small scale of the figures does not display such fine details except in his pl. 1, fig. 8, where transversely aligned endosperm cells are clearly seen around the basal scar. Endosperm structure is also clearly visible in two casts from Mokattam in the British Museum (V.13240 and V.13695; Pl. 11, figs. 7, 8).

The variable and considerable amount of compression of the seeds must be stressed, for some are almost reduced to thick concavo-convex lenticles (V.13240). Inevitably this crushing increases the diameter. V.13239 is obliquely distorted, the basal aperture having been forced into a basi-lateral position (Pl. 10, fig. 3).

As in the living, so also in the fossils, endosperm may show features not discernible on the interior of the testa represented by internal casts. V.13240, in addition to the typical transverse pattern of endosperm ridges (Pl. 11, fig. 8), shows on its flatter surface a band of elongate, longitudinally aligned endosperm cells which by comparison with the living have structural significance, probably indicating the position of the raphe. Towards, but well below, the apex a radial arrangement of the endosperm on this band suggests the point of entry into the endosperm of the fibres from the raphe (Pl. 11, fig. 7). On the more convex surface of this specimen, the coarse network of fibres seen in the living between the two integuments of the testa are faintly impressed (Pl. 10, fig. 5).

V.13239 has a mosaic pattern all over the surface. This may be the impression of a cracked testa which has peeled. But the important feature of this specimen is that sub-apically the cast shows a deep, small, funnel-shaped opening towards which fibre-impressions converge, and into which they pass (Pl. 10, fig. 4). Here the entry of the raphe fibres is clearly indicated. V.13695 shows a similar but more obscurely preserved radiating structure.

Thus these specimens illustrate a well-established fact, that owing to the maceration that fossils have frequently undergone, they may display structures which are more difficult to demonstrate in Recent material.

We must now return to the specimens named *Rubiaceocarpum markgrafi* Kräusel. As already stated on p. 159 these appear to be seeds (abnormally short and broad) with outer integument preserved. They have undergone considerable lateral compression.

Their form can be matched among the *Nipa* seed-casts illustrated by Kräusel

(1939, pl. 1, cf. figs. 8, 21; 18, 24; 16, 24; 17, 20). I have been able to examine the specimen illustrated in Krausel's fig. 24, which shows the base of the seed with its large aperture. A very interesting feature is a broad flat fibre band which half encircles the seed in the plane of symmetry (Pl. 11, fig. 9*f*). This resembles the raphe fibre described above in *Nipa fruticans*, although seed and fibre are on a larger scale. The fact that it is visible at the surface of the specimen must mean that some measure of abrasion had removed part of the spongy parenchyma. The superficial impressions of the transverse fibres of the endocarp have also been destroyed at the same time, traces only of them being visible in a few of the deeper furrows of the outer integument.

We may ask what relationship does this ribbed entity bear to its living analogue? It appears to be an internal cast of a hollow mould left by a seed which subsequently decayed. The filling of the hollow with limestone resulted in the characters impressed on the mould being reproduced on a cast, much as sealing-wax poured into the hollow mould of any fossil will reproduce its solid form. An actual replacement of the seed itself cell by cell would have given a far sharper representation of it, and in places at least would have provided evidence of cell-structure.

The ribbed seed shown by Kräusel (1939, pl. 1, figs. 20, 21) perhaps retained even more of the outer integument, for there are suggestions of transverse fibre impressions at the base of fig. 21, and the raphe band appears to be only partly uncovered.

The longitudinal striation on the ridges in Kräusel's pl. 1, fig. 1, may indicate that part of the outer integument of the testa is still present on this cast, which he referred to *Nipadites*. But suggestions such as this can only be verified by examination of the specimens themselves.

Reid & Chandler (1933 : 122) gave reasons for referring the London Clay fossils to *Nipa* rather than to *Nipadites*. They appear still to hold good. The most outstanding difference between living and fossil is the presence of the short longitudinal septum, which by partial subdivision of the locule in *N. fruticans* produces the only constant deep and conspicuous longitudinal furrow on the seed. This septum and furrow are absent in all the fossils. Nevertheless so closely identical with the living is the structure of the fossils in all other respects (even in smallest details) that the presence or absence of the septum still appears to the writer to have specific rather than generic value. Probably however, the real meaning of this character can only be decided by a detailed study of the developing ovary. It may, or may not, have a connection with the suppression of two out of the three original locules or ovules. In the meanwhile it is suggested that the name *Nipa* be used for the fossils.

DICOTYLEDONES

Family ANONACEAE

Genus *ANONASPERMUM* Ball *emend* Reid & Chandler, 1933

Anonaspermum aegypticum n. sp.

(Pl. 11, figs. 13–15)

DIAGNOSIS. Seed-cast oval or oboval in outline, much compressed with slight median depression ; rumination ridges close and narrow, extending from the depression to the margins, diverging from the depression at the distal end, occasionally forking near the margin, with a few short intermediate ridges. Four-partite in transverse section. Thickness only about half the greatest diameter in the plane of symmetry (15·5 mm.).

HOLOTYPE. A seed-cast, distal end, with testa almost entirely abraded (Pl. 11, figs. 13–15). Brit. Mus. (N.H.), No. V.31106.

LOCALITY AND HORIZON. Gebel Atshan, Kosseir Area, Red Sea ; Dano-Montian Lower Esna Shales.

DESCRIPTION. The unmistakable internal cast of a seed of Anonaceae showing typical ruminate albumen and marginal encircling band of raphe and chalaza (Pl. 11, figs. 13, 14). The hilar half of the seed is missing. The surviving fragment represents the distal end, which appears to have been severed from the proximal only a short distance above the middle of the specimen. The cast was originally oval or oboval in outline, bisymmetric, somewhat compressed at right angles to the plane of symmetry, anatropous with encircling raphe in the plane of symmetry. The raphe begins to broaden on one side where it merges into the linear chalaza (Pl. 11, figs. 13, 14 *ch.*). It completely fills the slight marginal groove at the edge of the albumen. Albumen having a median depression on each broad surface, ruminations forming narrow close ridges from the margin of the seed to the median depression. The ridges diverge from the end of the depression to the apex or distal end of the seed. The inner ends of opposite ridges do not unite at this point to form a series of curves as in *Anonaspermum commune* Reid & Chandler (1933 : 184, pl. 5, figs. 14–17). Short ridges of varying length sometimes arise at the margin and are interposed between the longer ones. Occasionally one of the longer ridges may divide into two towards the margin of the seed. The transverse section exposed on the fractured surface shows a four-partite arrangement of the albumen (Pl. 11, fig. 15). In the slight depressions in the middle of the broad surfaces part of the fibrous layer of testa is preserved (Pl. 11, fig. 13). On the four-partite sectioned surface oblong cells arranged in transverse rows at right angles to the plane of symmetry of the seed can be seen. The rows are about 0·028 mm. broad. The cells are partially obscured by sinuous fine striations lying parallel in a general way with the plane of symmetry. Parts of the ruminations as seen on the fractured surface of the seed are obscured by a thin brown mineral film which bears the impression of a thin but rough coat, the cells of which lie at right angles to the plane of symmetry. It represents the filmy inner integument which penetrated between the plates of albumen as in living seeds.

Actual length of seed preserved, 10 mm.; estimated length of complete seed, about 22 mm. Maximum diameter actually preserved in plane of symmetry, 14 mm.; probable measurement in the complete seed, about 15 to 15·5 mm. Diameter at right angles to plane of symmetry, 7 (at the centre) to 7·5 mm. (at each side).

REMARKS. The seed was clearly larger than any described from the London Clay, about twice the size of the largest there recorded. It was also relatively thinner at right angles to the plane of symmetry than any London Clay species with albumen forming superficial ridges. Similar divergence of the ruminations at the distal end is seen in *A. rugosum* and *A. pulchrum* Reid & Chandler (1933 : 186, 187, pl. 5, figs. 21–27), but not in *A. commune* and *A. rotundatum* Reid & Chandler (1933 : 184–187, pl. 5, figs. 14–20).

Although imperfect, this solitary specimen appears to be sufficiently distinctive to merit a specific name. It is described as *Anonaspermum aegypticum*. The family Anonaceae is almost exclusively tropical today, occurring in both hemispheres. It is recorded from both hemispheres in Eocene times also.

Family EUPHORBIACEAE

Genus ***LAGENOIDEA*** Reid & Chandler *emend.*

Since the first description of this genus was published (Reid & Chandler, 1933 : 493–497) a few small but important new facts have come to light which make it necessary to correct the diagnoses and descriptions then given. The information was derived from additional London Clay material of *Lagenoidea trilocularis*. The diagnosis should now read :

Fruit a superior, syncarpous, loculicidal and septicidal capsule, two to four-loculed, locules single-seeded. Pericarp thick, formed of radially aligned cells, seeds pendulous, radially compressed, anatropous, raphe ventral, chalaza basi-ventral.

TYPE SPECIES. *L. trilocularis* Reid & Chandler.

The recent discovery that the seeds are pendulous with ventral raphe now makes it possible to refer the genus *Lagenoidea* to the family Euphorbiaceae. Formerly such a relationship was considered impossible, for the seeds were then believed to be erect and orthotropous owing to the fact that the raphe is slender and difficult to detect when it is preserved at all.

The shape of the fruit and the combined loculicidal and septicidal dehiscence is typical of the Euphorbiaceae. This was recognized by Ettingshausen when he labelled one specimen (V.23129) *Euphorbiophyllum eocenicum* (see Reid & Chandler, 1933 : 495, pl. 29, fig. 6). This specimen was never described or figured as such, hence the inappropriate name *Euphorbiophyllum* need not be retained for these fruits. It has not yet been possible to connect them with a living genus, but the relationship must be sought among those sections of the Euphorbiaceae with single-seeded locules having locule-linings formed of complicated interlocking cells. Attenuated obovate seeds are rare in the family but obovate seeds may occur, e.g., in *Chaetocarpus* where the seeds may remain attached to the inner angle of the carpel wall when the external valves have fallen away.

Lagenoidea trilocularis Reid & Chandler

(Pl. 12, figs. 16–20)

1933. *Lagenoidea trilocularis* Reid & Chandler, p. 493, pl. 29, figs. 1–18.

The revised diagnosis of this species based on London Clay material as stated above should read:

Fruit: Sub-globular, three- (rarely four-) loculed; capsule splitting loculicidally and septicidally into six (rarely eight) segments. Length, 7 to 14 mm.; diameter, 8 to 23 mm.; length of locule-cast (= seed), 3·5 to 4·5 mm.; greatest diameter, 2 mm.; least diameter, 1 mm.

LOCALITY AND HORIZON. Gebel Atshan and Gebel Durvi, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

MATERIAL. Two fruits, one with hollow interior. Brit. Mus. (N.H.), Nos. V.31107–08.

DESCRIPTION AND REMARKS. Two fruits, neither of which show internal structure. One (Pl. 12, figs. 16–18) shows a thin wrinkled epicarp partly hiding the surface of the capsule, but the six segments can be clearly distinguished. A sub-circular basal scar indicates the former extent of the calyx (Pl. 12, fig. 17). Length of fruit, 10 mm.; transverse diameter, 9 by 11 mm.

The second fruit (Pl. 12, figs. 19, 20) also shows the six valves and basal scar, but its surface is somewhat encrusted and is therefore rather obscure. The interior is hollow, while there is a hole at the attachment through which the seeds may be presumed to have escaped. Length of fruit, 11 mm.; diameter, 14 by 12·5 mm.

Lagenoidea bilocularis Reid & Chandler

(Pl. 12, figs. 21–23)

1933. *Lagenoidea bilocularis* Reid & Chandler, p. 496, pl. 29, figs. 19–27.

LOCALITY AND HORIZON. Gebel Atshan, Kosseir Area, Red Sea. Dano-Montian Lower Esna Shales.

MATERIAL. Two typical fruits. Brit. Mus. (N.H.), No. V.31109.

DESCRIPTION. Two sub-ovoid somewhat laterally compressed fruits showing six external longitudinal grooves delimiting the valves and septum. The narrow median opposite segments between the pairs of lateral segments mark the edges of the septum. The pairs of end segments are bounded by planes of loculicidal and septicidal splitting. As in the London Clay fruits of this species the pairs of valves may be presumed to overlie the two locules.

The stylar scar is seen at the narrow end in both fruits and the attachment scar is preserved at the broad end in the smaller specimen. Unfortunately the internal structure is not exposed. There can be no doubt however that the fruits are identical with the London Clay species *Lagenoidea bilocularis* Reid & Chandler.

Length of the two endocarps, 11 and 9·5 mm.; greatest diameters, 11 and 9 mm.; least diameters, 6 and 5·5 mm. respectively.

Family EUPHORBIACEAE ?

Genus ***PALAEOWETHERELLIA*** nov.

DIAGNOSIS. Fruit sub-globular, syncarpous, with more than five carpels; dehiscence loculicidal and septicidal, locules radially arranged, tangentially compressed; placentation axile; seeds solitary in each locule, occupying part only of the plane of the locule; pendulous by long arched funicles which arise some distance below the apex of the fruit. Pericarp parenchymatous. Seeds slightly inflated, obovate in outline, beaked at the micropyle, anatropous with ventral raphe. Testa one cell thick, formed of equiaxial cells.

TYPE SPECIES. *P. schweinfurthi* (Heer).

Palaeowetherellia schweinfurthi (Heer) Chandler

(Pl. 12, figs. 24–30; Pl. 13, figs. 31–38; Pl. 14, figs. 39–47; Pl. 15, fig. 48; Text-fig. 1)

1876. *Diospyros schweinfurthi* Heer, p. 6, pl. 1, figs. 1–10.
1876. *Royena desertorum* Heer, p. 10, pl. 1, figs. 11–16.
1889. *Diospyros schweinfurthi* Heer: Schenk, p. 745, text-fig. 384^{7-13}.
1889. *Royena desertorum* Heer: Schenk, p. 745, text-fig. 384^{14-18}.
1939. *Diospyros schweinfurthi* Heer: Kräusel, p. 106, pl. 2, figs. 9, 10; text-fig. 32.
1939. *Royena desertorum* Heer: Kräusel, p. 106.

DIAGNOSIS. Fruit shorter than broad, 6 to 9, 10 or even 12-loculed. Funicles arising from the axis at about one-third to one-half the length of the fruit from the apex, passing between the closely opposed surfaces of the locule above the seed. Seed so obliquely placed as to lie almost transversely with the hilum upwards towards the circumference of the fruit, and the ventral margin parallel with the arched funicle. Fine parenchyma which forms the bulk of the carpel wall enclosing numerous patches of coarser cells very liable to decay associated with a system of fibres near the surface of the endocarp. Diameter of endocarp, 17 to 22 (or ? 24) mm.; length about 7·5 to 10 mm. Maximum length of fruit with exocarp preserved, 14 mm.

NEOTYPE. A nine-loculed fruit (Pl. 13, figs. 31–37). Figured Kräusel, 1939, pl. 2, figs. 9, 10 ; text-fig. 32. Brit. Mus. (N.H.), No. V.12985.

LOCALITIES AND HORIZONS. Farafra, Egypt ; Lower Danian (Upper Cretaceous). Gebel Tarawan and Gebel Um-el-Ghanaim, Kharga Oasis, Egypt ; Dano-Montian Lower Esna Shales. Gebel Atshan, Gebel Durvi and Abu Tundub, Kosseir Area, Red Sea ; Dano-Montian Lower Esna Shales.

DESCRIPTION. *Fruit:* Having an exocarp (leathery ? but usually abraded) about 1·6 mm. thick, its surface more or less smooth but the details of its structure obscured by mineral incrustation (Pl. 12, fig. 27 ; Pl. 14, figs. 42, 43). It encloses a syncarpous multilocular endocarp, circular or sub-circular in outline, sometimes slightly angled over the locules, depressed dorsiventrally, usually somewhat flattened at the apex, either slightly pointed below or somewhat excavated (Pl. 12, figs. 24–26 ; Pl. 13, figs. 31, 32).

The style base may be marked by a small inconspicuous scarcely prominent circular scar (Pl. 13, fig. 31), but this is not usually apparent. External surface with radial ridges or sutures which correspond with the locules. Alternating with them are less conspicuous ones which overlie the septa ; they are not invariably seen, and are most marked in much abraded specimens or in those which have started to split septicidally (Pl. 12, figs. 25, 29, 30). Dehiscence conspicuously loculicidal, less obviously septicidal. Possibly the septicidal planes of weakness are cemented by infiltration of mineral substance as they are normally so inconspicuous. Carpels 6 to about 12, radially arranged about the axis of the fruit (Pl. 12, figs. 24–26 ; Pl. 13, figs. 31, 32), unequally developed in some specimens so that complete fruits may show perfect or imperfect radial symmetry. V.12985, for example, shows unequal development at opposite ends of one diameter, two of the smaller carpels are evidently abortive, but their existence is clearly revealed by a longitudinal fracture of the fruit (Pl. 13, figs. 33–36). One of Heer's transversely sectioned specimens (1876, pl. 1, fig. 9) in which he only recognized 8 locules clearly shows 9 in the figure, 2 being abortive or ill-developed. Up to the present the least number of carpels seen is six (Pl. 12, figs. 24, 25). Fibres of the fruit axis fused with the surrounding parenchyma not occupying a distinct central canal. Locules extend from the axis to the periphery of the fruit, but are tangentially compressed and so completely flattened around their edges that the two flat surfaces are contiguous. The seeds are neither as long nor as broad as the locules. It is only where the seed actually lies that there is a slightly inflated cavity equal to the thickness of the seed (Pl. 13, figs. 32–36 ; Pl. 15, fig. 48). Placentation axile. Seeds solitary, suspended by long arched funicles which spring from the axis at about one-third or one-half of the length of the fruit from the apex. From the point of emergence of the funicle from the axis (Pl. 13, figs. 33–37 ; Text-fig. 1D) to the point where it passes into the seed at the hilum it lies within that part of the locule where the opposed walls are contiguous. The longer axes of the seeds lie at an angle of 60° or thereabouts to the axis of the fruit, hence the position of the seeds is oblique or almost transverse in the fruits. As this is a consistent feature it must be original. Owing to this peculiarity, the dorsal surface of the seed lies towards the base of the fruit, the hilar end is directed outwards and upwards, the distal end lies close to the lower end of the fruit axis, and the ventral margin is uppermost, lying parallel with the long arched oblique funicle.

Pericarp of three layers: (1) a leathery (?) exocarp of fine parenchyma whose surface is obscure, but in section it can be seen in one place to be formed of rounded more or less equiaxial cells about 0·028 mm. in diameter. (2) A compact parenchymatous coat which constitutes the main thickness of the endocarp. It is greatly thickened in the part of the fruit between the flattened margins of the locules. The outermost part of the endocarp is formed of close fine parenchyma which is rather readily abraded. Superficially, when the coat is weathered, the cells can be seen to be arranged in radiating groups. Possibly there is a fibre at the centre of each group. Differential weathering of this coat produces a series of rugosities having the effect of a coarse network, the centre of each radial group being sunk below the general level of the surface. Beneath the layers of radially grouped cells comes the main thickness of the endocarp. It is formed of equiaxial cells about 0·02 mm. in diameter. Within it are numberous patches of coarse angular parenchyma, with cells about 0·05 to 0·1 mm. in diameter, developed most conspicuously near the outer surface of the coat. These patches also may have a thin fibrous core fed by fibres visible near the periphery on the flat surfaces of the loculicidally fractured carpels (Pl. 12, fig. 30; Pl. 13, fig. 35). Here loops are seen from which branches are directed inwards to the centre of the endocarp, while more numerous and finer branches are directed outwards to its external surface.

V.12985 had laid long exposed before fossilization, and the coarse parenchyma patches have decayed more readily than the more compact tissue which surrounds them. Their decay has produced deep funnel-shaped cavities with circular orifices which form a conspicuous feature at the surface of the endocarp. They are best shown on the lower surface, where they occur in more or less longitudinal rows (Pl. 13, fig. 32). The whole surface of this specimen (as preserved) has been highly polished by the abrasion it has undergone.

(3) The innermost carpellary coat is a smooth locule-lining formed of small cells arranged so as to produce straight or slightly sinuous or criss-cross lines or striations with a general transverse or oblique orientation. The distance between the striae is about 0·02 mm. The striate lining is seen to the left of the axis in Pl. 13, fig. 36, and is more clearly visible on the specimen itself and on the surface of the abortive locule-cast.

There is some reason to think that that part of the thick parenchymatous coat which was in contact with the locule-lining was rather spongy in texture, or that it was at least softer and less resistant to decay than the layers outside it. In places it is partially decayed, while in other places it appears obscurely columnar in transverse section (Pl. 13, fig. 35, to the left of the fertile locule-cast). It clings in patches to the locule-cast, giving the appearance at first sight of a warty testa formed of fine angular, parenchymatous cells (Pl. 13, fig. 35; Pl. 14, fig. 41). But careful scrutiny reveals its true nature. The decay is most conspicuous around the axis at the base, exposing the locules and seeds in some specimens (Pl. 12, fig. 26; Pl. 13, fig. 32). Length of fruit, 7·5 to 9·5 mm.; transverse diameter, 17 to at least 22 (? 24) mm. Length of V.12985, 8 mm.; diameter, 19 mm. Length of specimen shown in

Pl. 14, figs. 42, 43, with exocarp preserved, 14 mm.; estimated diameter, 24 by 17 mm. Length of another fruit, 10 mm.; diameter, 22 mm.

Seeds (Pl. 13, figs. 33, 35, 37; Pl. 14, figs. 40, 41, 43–47; Pl. 15, fig. 48): More or less obovate in outline, very slightly inflated, with a small beak-like projection at the hilar end which carries the micropyle. This organ is indicated by the radial alignment of the cells at its tip. That the radicle probably lay within the beak is suggested by its shape. The general symmetry indicates an anatropous seed with hilum in the concavity which delimits the " beak " from the main body of the seed, i.e., closely adjacent to the micropyle. Here the funicle is seen to enter the seed (cf. Pl. 12, fig. 28; Pl. 13, fig. 35). Raphe marginal, ventral, indicated by the form of the seed as well as by a shallow marginal groove at the rounded end opposite to the micropyle. The groove ends on the dorsal surface. Its termination probably indicates the position of the obscure chalaza.

On the rounded end of the best developed seed exposed by abrasion within a locule-cast of V.12985 the chalaza is probably marked by a small deep depression in the same position (i.e., at the lowest point of the seed as it lay in the fruit). If so this is the cast of the raphe fibres, where they turn sharply inwards to enter the seed or albumen.

Testa apparently only one cell thick, since the cells of the external and internal impressions appear to agree exactly in size and character. It was formed of equiaxial polygonal angular cells about 0·025 to 0·03 mm. in diameter, convex externally (as shown by the concave external impressions on a small fragment of external cast seen in the specimen figured in Pl. 14, figs. 42–47), concave internally (shown by the convex impressions on the internal casts of the seed figured in Pl. 14, figs. 39–47). Dimensions of seeds: Length, 5·5 to about 7 mm.; breadth, 4 to 5 mm.; thickness, 1 to 1·5 mm.

REMARKS AND AFFINITIES. In examining and interpreting mineralized fruits it is necessary to remember that mineral substance in solution may percolate through all incipient fissures as well as into actual cavities. On evaporating and hardening it may then form a cement which prevents or hinders separation of parts along natural planes of weakness. But in that the film of cement may often be incomplete, indications of natural dehiscence can usually be detected. Thus in *Wetherellia* (Reid & Chandler, 1933: 251), while many specimens were so cemented that their loculicidal dehiscence was concealed, the fruits were found in such large numbers that plenty of evidence as to their natural manner of splitting was available. In the fossil just described septicidal dehiscence may be obscured in a similar way. The mineral cement may cause adhesion of surfaces and tissues which in life, or at least after maceration, whether natural or artificial, would separate readily. For example, in *Palaeowetherellia*, a locule-cast may simulate a seed (which it covers and conceals), and patches of endocarp adhering to the cast but torn from adjacent tissues may look like testa (cf. Pl. 13, fig. 35; Pl. 14, fig. 41). Again thin films of cement between delicate tissues may reproduce as external or internal impression coats which could scarcely have escaped destruction, e.g., the delicate one-cell thick testa of *Wetherellia* and *Palaeowetherellia*.

Palaeowetherellia is now known from more than a dozen specimens. In addition to those figured by Heer (1876) as *Diospyros*, ten more, five of which are incomplete, are now available. These will be catalogued below with details of any special features they show and a note of the place of origin.

The best preserved for study was described and figured by Kräusel (1939 : 106, pl. 2, figs. 9, 10 ; text-fig. 32) as *Diospyros schweinfurthi* Heer. Certain of its characters, including the number of locules, were obscure at the time, but have since been clearly shown by the beautiful section (largely a natural fracture surface) now exposed (cf. Pl. 13, figs. 33–37). On this section most of the newly recorded details are based. Two other specimens from the Kharga Oasis have yielded additional data, thanks to their broken condition, and have made it necessary to unite *Diospyros schweinfurthi* Heer and *Royena desertorum* of Heer as a single species (cf. p. 176). Other fruits or fragments from Kosseir throw light on the variation in the number of locules, the branching of fibres of the endocarp, mode of dehiscence, variations of size, and character of exocarp.

The new evidence makes it impossible any longer to refer this species to the family Ebenaceae in spite of some superficial resemblances to *Diospyros*. In this genus the soft pulpy fruit breaks irregularly ; its radially arranged locules (with coarse striae) have no flattened area where the two opposed surfaces are in contact. The seeds are pendulous on short funicles which spring from the upper inner angles of the locules arising at the top of the fruit axis (Text-fig. 1A). The anatropous seeds have a conspicuous superficial *dorsal* marginal raphe which does not terminate at the chalaza (i.e., at the opposite end of the seed to the hilum) but is continued along the ventral margin so as to encircle the seed. It gradually tapers, dying out finally close to the hilum. The seeds lie vertically in the locules with their ventral margins parallel with and close to the axis. They are not beaked like those of the fossil but the terminal micropyle usually leads into a large conspicuous canal produced by incurving of the testa. The radicle of the embryo occupies this canal, which on an internal cast of the seed would appear as a conspicuous deep depression or pit (Text-fig. 1E) with a projection from its base representing the cast of the radicular pocket. Similar features are characteristic of *Royena*, which resembles the fossil even less than *Diospyros* in the form and fewness of its seeds. One other characteristic may be noted, namely the cell-structure. In *Diospyros* the testa cells, while they may be similar in style to those of the Egyptian fossil, are *convex* internally, so that on an internal seed-cast they would produce concave instead of convex impressions. Unfortunately it has not yet been possible to find any living closely allied genus, although a suggestion will be made below as to family relationship. But there can be no doubt at all that *Palaeowetherellia* closely resembles the fossil genus *Wetherellia* Bowerbank from the London Clay in its form, placentation, locule characters, seeds, and cell-structure, and in the tendency for dissolution of the carpel to occur at the centre which allows the seeds to escape through the gaps thereby produced—a point noted by Bowerbank in describing *Wetherellia*. Similar decay may be seen in crab apples which have lain long on the ground in winter. A detailed description of *Wetherellia variabilis* was given by Reid & Chandler (1933, 251, pl. 9, figs. 7–22). A second species—*W. dixoni* (Carruthers)—has since been recognized from the Cuisian (?)—or it may be Lutetian or Auversian—of Selsey.

Its full description awaits publication. The characters of these two species of *Wetherellia* are summarized in a table below.

	Wetherellia variabilis Bowerb.	*Wetherellia dixoni* (Carr.)
Fruit :	A syncarpous 2 to 5-loculed septicidal capsule or schizocarp, later splitting loculicidally. Sub-globular to ovoid with length equal to, greater, or less than the diameter. Smooth, ribbed, or angled externally.	A syncarpous 5 to 7 (or more ?) loculed capsule splitting septicidally and loculicidally. Sub-globular but somewhat dorsiventrally compressed. Longitudinally ribbed externally. Septal fibres apparently give rise to hollow external spines.
Locules :	Radially arranged around a central axis which extends throughout the length of the fruit. Tangentially compressed so that the opposed walls are contiguous except where the seed lies.	As for *W. variabilis*.
Placentation :	Axile; solitary seeds suspended on long arched funicles which spring from the axis at a point about one-third or one-quarter of the length of the fruit from the apex. The funicles lie within that part of the locule where the opposed walls are contiguous.	As for *W. variabilis* except that the funicles spring from the axis at a point about one-sixth to two-sevenths of the length of the fruit from the apex.
Seed :	Slightly oblique, with the distal end nearer to the axis than the proximal.	As for *W. variabilis*, but the seeds somewhat broader in proportion to their length.
Pericarp :	Of thick angular parenchyma. Locule-lining smooth and shining, obliquely or transversely and finely striate.	As for *W. variabilis*.
Dimensions of fruit :	Length, 12 to 20 mm. Diameter, 12 to 24 mm.	Length, 4 to 7 mm. Diameter 13·5 to 15 mm. (somewhat dorsiventrally crushed).
Seed :	Scarcely inflated, elongate obovate in outline; slightly beaked at the narrow hilar end, anatropous; hilum terminal, raphe ventral, micropyle adjacent to the hilum; chalaza small and inconspicuous at the opposite end to the hilum. Testa thin, a single layer of angular equiaxial cells convex externally, concave internally, 0·03 to 0·05 mm. in diameter.	As for *W. variabilis*, but somewhat shorter and broader. Raphe fibres not actually seen. Testa not seen.
Dimensions of typical seeds :	12 × 3·75 × 1·5 mm.	(1) 5·5 × 4 × 1 mm. (2) 7 × 4·75 × 1·5 mm.

It may be noted that the parenchymatous tissues of both *Wetherellia* and of the Egyptian fruits is evidently very liable to decay, for partial destruction of the centre of the fruit has occurred in both so that the locules are exposed, allowing the seeds to escape. Consequently locules which have not dehisced in the normal way may be empty.

While therefore *Wetherellia* and the Egyptian fossils show a striking measure of agreement such as suggests a family relationship, their characters are sufficiently distinctive to indicate a generic difference between them. The name *Palaeowetherellia* is here suggested for the Egyptian fruits, which thus become *Palaeowetherellia schweinfurthi* (Heer).

The distinctions so far as they are known at present may be summarized in tabular form.

Wetherellia	*Palaeowetherellia*
Septicidal capsule or schizocarp, also splitting loculicidally. Locules 2 to 7 (or more ?).	Loculicidal capsule also splitting septicidally. Locules 6 to about 12.
Long arched funicles springing from the axis at one-sixth to one-third of the length of the fruit from the apex.	Long arched funicles springing from the axis at one-third to one half the length of the fruit from the apex.
Seed lying slightly obliquely in the locule with the distal end nearer to the axis than the proximal.	Seed so obliquely placed as to be almost transverse, with the proximal end towards the outer edge of the fruit and the distal end near the lower end of the axis.
Seeds scarcely inflated, oval to elongate obovate in outline, beaked at the narrow end. Hilum terminal.	Seeds slightly inflated, obovate in outline, beaked at the narrow end. Hilum almost terminal just below the beak on the ventral margin.

In 1933 Reid & Chandler referred *Wetherellia* to the family Linaceae but it is necessary to correct this ascription on the following grounds:

(1) More than five locules are now known to occur in undoubted *Wetherellia* (*W. dixoni*).

(2) As noted in 1933 the coat of *Hugonia* (Linaceae) with which *Wetherellia* was compared is fibrous, that of *Wetherellia* and of *Palaeowetherellia* is consistently parenchymatous with a few scattered fibres.

(3) The seed in *Hugonia* occupies more of the locule than the seed of *Wetherellia* or *Palaeowetherellia*.

(4) The funicle is short and straight in *Hugonia*, not long and arched as in *Wetherellia* and *Palaeowetherellia*.

(5) Polygonal cells of the testa are much finer in *Hugonia* than in *Wetherellia* or *Palaeowetherellia*.

(6) The chalaza of *Hugonia* forms a large conspicuous scar unlike the inconspicuous scarcely distinguishable chalaza of *Wetherellia* and *Palaeowetherellia*.

Taken together these differences appear on maturer reflection to be such as to distinguish *Wetherellia* and *Palaeowetherellia* from Linaceae.

The true relationship of the fossils therefore remains to be discovered. They may belong to an extinct family whose nearest living allies have not yet been traced. But certain features point to Euphorbiaceae as a possible alliance. These features are the combination of loculicidal and septicidal dehiscence common in capsules of Euphorbiaceae, the number of radially arranged locules, and their tangential compression—such an arrangement is present in *Hura*—and the point of origin of the funicles from the axis which may be well below the apex of the fruit in many Euphorbiaceae. Pendulous seeds solitary in the locules with ventral raphe. At the same time it must be frankly admitted that no really comparable genus has yet been discovered, so that attribution to Euphorbiaceae must be regarded as doubtful. But no other known family shows so many of the characters of the fossil as the Euphorbiaceae.

MATERIAL.

Fruit (Pl. 13, figs. 31–37). Also figured Kräusel (1939, pl. 2, figs. 9, 10; text-fig. 32). Neotype.

A nine-loculed fruit now fractured longitudinally to show one fertile and one abortive locule, the median axis and mode of placentation.

Cell patches of the inner carpellary layers adhere to the fertile locule-cast giving it a roughened granular appearance which at first sight simulates a rough testa (Pl. 13, figs. 33, 35). The elongate cells or striations of the locule surface are visible on the abortive locule-cast and the locule wall between it and the axis (Pl. 13, figs. 34, 36). The base of the specimen has decayed probably through long exposure before fossilization, displaying locules, locule-casts and seeds (Pl. 13, figs. 32–34). The carpel wall has also suffered from differential decay, which has produced deep superficial pits originally occupied by coarse-celled tissue especially on the lower surface (Pl. 13, fig. 32). Incipient loculicidal splitting is visible on one radial rib at the apex of the fruit (Pl. 13, fig. 31). Diameter, 19 mm.; height, about 8 mm. (somewhat reduced by decay at the base).

From the Lower Danian (Upper Cretaceous); Farafra, Egypt. Brit. Mus. (N.H.), No. V.12985.

Part of a fruit (Pl. 13, fig. 38; Pl. 14, figs. 39–41).

A wedge-shaped loculicidal segment of a fruit bounded by the external surface on one side, and by two adjacent locules on its two lateral faces. The inner end of the wedge (fruit wall and axis) has broken or decayed, leaving exposed the locule and seed-casts projecting inwards (Pl. 14, fig. 40). Tangential breadth of segment, 6·5 mm.; height, 7·5 mm. Radius from centre (as preserved) to outer edge, 7·5 mm. Estimated breadth of fruit, about 17 mm. Length of seed or locule-cast, 5·5 mm.; breadth, 4 mm.; thickness, 1 mm.

The exocarp is not preserved, the surface of the capsule is rough, not differentially decayed before fossilization as in V.12985. The substance is parenchyma with cells about 0·02 mm. in diameter in which patches of coarser parenchyma (cells about 0·05 mm. in diameter) are embedded. The decay of such coarse patches produced the deep pits in V.12985.

The locule-casts narrow to the exterior and are directly slightly upwards, at first sight suggesting parietal placentation. One was more fully displayed by removal of a few adherent fragments of the opposed carpel wall. Some of the parenchyma cells of the wall adhere at this narrow end of the locule-cast producing the effect of a rough nodular testa (Pl. 14, fig. 41).

Nearer the inner end of the locule abrasion has removed first the parenchymatous cells of the carpel and then a layer of locule-cast, thereby exposing the seed-cast (Pl. 14, fig. 41 *sc.*), with its angular equiaxial convex cell-impressions about 0·025 to 0·03 mm. in diameter (hence cells were concave inwards on the testa).

The testa is also represented by fragments of its external impression showing the same cell-impressions which are concave on this surface (hence the external surface had convex cells).

This fruit segment is clearly identical in character and size with Heer's figure of *Royena desertorum* (1876, pl. 1, figs. 11–16). But the details of its cell-structure and the arrangement of its locules also unite it with V.12985 and with another specimen figured in Pl. 14, figs. 42–47 ; Pl. 15, fig, 48. Hence this imperfect fruit constitutes a most important link in the evidence which unites *Royena desertorum* with *Palaeowetherellia schweinfurthi* (Heer).

From the Dano-Montian Lower Esna Shales ; Gebel Um-el-Ghanaim, Kharga Oasis, Egypt. Brit. Mus. (N.H.), No. V.31114.

A perfect six-carpelled endocarp (Pl. 12, figs. 24, 25) with base intact. The loculicidal sutures are clear, the septicidal more obscure except where abrasion has removed the outermost layers. The whole upper surface has been somewhat abraded showing the radiating groups of fine parenchyma. Diameter, 17 mm. ; length, 9·5 mm. Brit. Mus. (N.H.), No. V.31110.

A seven-partite endocarp, slightly asymmetrically developed. It is somewhat corroded on one side so that a seed (or locule-cast) is partially exposed. The exocarp is almost entirely abraded, one small patch only persisting at the base. The surface of the endocarp is also much abraded. The whole specimen is encrusted with mineral deposit which forms small pimples over the exposed fibre ends and coarse cell patches. Diameter, 17 mm. ; length, 10·5 mm. M. I. Youssef Collection, 1952.

Two segments of an endocarp showing the cavities of two locules. The lines of loculicidal dehiscence can be detected. The surface is somewhat abraded, exposing the irregular rugosities due to the radiating clusters of cells just below. A seed-cast in the locule between the two segments shows clear evidence of the ventral raphe. M. I. Youssef Collection, 1952.

The above three specimens are from the Dano-Montian Lower Esna Shales ; Gebel Atshan, Kosseir Area, Red Sea.

An eight-loculed endocarp (Pl. 12, fig. 26), perfect except for decay at the centre of the base so that the inner angles of the locules are exposed. The septa show median planes of weakness as for septicidal dehiscence. Five locules have retained their seeds, some of which are abortive; from the others the seeds have fallen through the gap caused by the decay above described. No exocarp is preserved, and there is considerable mineral incrustation over the surface of the abraded endocarp. Hollows for the fibre ends are visible on the lower surface; a few encrusted rounded knobs probably indicate their position on the upper surface.

Half of a fruit (Pl. 12, figs. 27, 28) which has been fractured longitudinally through two of the locules. One has a locule-cast preserved, in the other the locule-cast is missing, but the funicle (now much encrusted with a mineral deposit) is seen. There appears to be evidence of seven locules on this fragment, so that the complete fruit must have had at least eleven or twelve locules. Adherent remains of exocarp are seen at the base and apex only and are shown in section where the coat has broken away from the endocarp. Exocarp and endocarp are much encrusted by a mineral deposit. On the endocarp the encrusted remains of the fibres described on p. 170 form small rounded prominences.

Half of an endocarp which has split longitudinally (Pl. 12, figs. 29, 30). Three and a half carpels are preserved and the septicidal and loculicidal fracture lines are clearly visible.

The half carpel has split both loculicidally and septicidally and has been pushed out of position. The surface is sufficiently abraded to expose the radial grouping of the small cell-clusters. The network of fibres is obvious on one loculicidal suture plane, although owing to the adherent parenchyma and secondary incrustation the fibres are not themselves exposed but their position is very apparent. No exocarp is preserved. Diameter of endocarp, 18 mm.; length, 9 mm. A few small shell casts and impressions adhere to one fracture plane.

The above three specimens are from the Dano-Montian Lower Esna Shales; Abu Tundub, Kosseir Area, Red Sea. Brit. Mus. (N.H.), Nos. V.31111–13.

A fruit (Pl. 14, figs. 42–47; Pl. 15, fig. 48) with exocarp preserved but cracked in such a manner that at first sight it simulates three perianth segments (Pl. 14, fig. 42). Actual diameter (incomplete because the specimen had been polished on one side at *p* in figs. 42, 43 thus showing a tangential section), 18 × 17 mm. Estimated complete maximum diameter (distorted), about 24 × 17 mm. Height, 14 mm.

The whole fruit is cracked through desiccation and crushing, and is held together by calcite cement (white in the figures). On the polished surface two seeds can be seen, one in transverse and one in oblique section. The first shows the seed-cast (*sc*) surrounded fairly closely by the locule-cast (*lc*) (Pl. 15, fig. 48), which is embedded in the pulp or parenchyma of the carpel. The base of the fruit is sunk, and broken along one radius so that a beautiful seed-cast was exposed, at first held in place by calcite cement, but later becoming detached (Pl. 14, figs. 43–47). The beaked end of the compressed ovate cast was directed outwards and upwards in the locule as in the section of V.12985 shown in Pl. 13, figs. 33, 35, 37.

Length of seed-cast, 7 mm.; breadth, 4·75 mm.; thickness, 1·5 mm.

Surface of cast with equiaxial slightly convex cell-impressions. Their divergence at the beaked end indicates the micropyle. A shallow marginal furrow at the opposite rounded end of the cast dies out on the dorsal surface (close to an accidental fracture line). It indicates the inner end of the raphe, its termination marking the site of a small inconspicuous chalaza.

From the Dano-Montian Lower Esna Shales; Gebel Tarawan, Kharga Oasis, Egypt. Brit. Mus. (N.H.), No. V.31115.

Two segments of an endocarp showing the cavities of three locules. The carpel wall between the two segments is abraded so that the seed-cast is exposed along its dorsal margin. When the segments are separated the chalaza can be detected at the lowest point of the seed-cast as it lies in the endocarp.

The exterior of the endocarp is also abraded, so that in places the inner thick layer of fine parenchyma is exposed. Remains of the outer layer with radiating cell clusters occur in patches, but are much obscured by mineral incrustation. Length of endocarp, 8 mm.; maximum breadth across the two loculicidal segments, 14 mm.

From the Dano-Montian Lower Esna Shales; Gebel Durvi, Kosseir Area, Red Sea. M. I. Youssef Collection, 1952.

Family Icacinaceae

Genus ***ICACINICARYA*** Reid & Chandler, 1933

Icacinicarya youssefi n. sp.

(Pl. 15, figs. 49–51)

Diagnosis. Fruit and endocarp almond-shaped or sub-obovoid in outline, lenticular in transverse section. External surface of endocarp with a series of more or less discontinuous irregular rugosities, some longitudinal, others transverse or oblique. Cells of endocarp markedly sinuous or coarsely digitate. Length of endocarp, 31 mm.; breadth, 22 mm.; thickness, 10 mm. Length of a fruit, 33 mm.; breadth, 26·5 mm.; thickness, 13 mm.

Holotype. Endocarp figured Pl. 15, fig. 51. Brit. Mus. (N.H.), No. V.31117.

Localities and horizon. Gebel Atshan and Gebel Durvi, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

Description. *Fruit* (Pl. 15, figs. 49, 50): Bisymmetric, somewhat compressed, giving a lenticular transverse section, obovoid in outline, slightly mucronate at the apical style, attachment at the opposite extremity to the style. Surface much puckered as if by shrinkage of the mesocarp, but having a few rather ill-defined longitudinal ridges which may branch or anastomose halfway up. They may be due to fibres in the pulp or just beneath the epicarp. The actual epicarp itself is probably missing. One margin (overlying the funicle ?) thicker than the other with two or three marked longitudinal ridges. Whole surface with a pattern of small, rounded or quadrangular depressions, about 0·5 to 1 mm. in diameter, arranged in longitudinal rows. Finer structure of digitate or markedly sinuous cells. The convergence of the ornamentation at the two ends indicates the position of style and attachment described. Length of fruit, 33 mm.; breadth, 26·5 mm.; thickness, 13 mm.

Endocarp (Pl. 15, fig. 51): Similar in form to the fruit, base narrowed to a point where the opening for the funicle is clearly seen. A ridge due to splitting followed by mineral infiltration is seen at the apical style. This tendency to split at the stylar end has been observed in other Icacinaceae, e.g., *Natsiatum eocenicum* Chandler from the Lower Headon of Hordle.

As in genera of Icacinaceae one margin is much thicker and more rounded than the other. Experience has shown that the thick margin carries the funicle but no section is available, so this cannot be verified in the present instance. External surface with an obscure pattern of small mostly discontinuous rugosities, some elongate and longitudinally aligned. They do not produce a definite network of ridges and hollows as in *Icacinicarya platycarpa* Reid & Chandler (1933: 345, pl. 16, figs. 11–18).

Surface of endocarp formed of small digitate or conspicuously sinuous cells with a tendency to transverse alignment. They are about 0·114 mm. broad and 0·057 mm. in length. Length of endocarp, 31 mm.; breadth, 22 mm.; thickness, 10 mm.

REMARKS AND AFFINITIES. Two specimens which by their general similarity may be presumed to belong to the same species although one shows the whole fruit, the other the endocarp only. One surface of the fruit shows the outline of a closely comparable endocarp owing to the contraction on drying which the pulpy exocarp has undergone (Pl. 15, fig. 50).

Although the most conclusive diagnostic characters of Icacinaceae can only be inferred because the unbroken character of the specimens conceals them, there can be little doubt of the relationship. The specimens are considerably larger than *Icacinicarya platycarpa*, which they resemble in their form, but as pointed out above, they can also be distinguished from that species by surface ornamentation. The cells of the endocarp are considerably larger than in that species and differ in their digitate form.

Although further information about this species is much to be desired, it is sufficiently well defined to be recognizable again, so that the specific name, *Icacinicarya youssefi*, after the finder, has been given.

Family ICACINACEAE ?

ICACINICARYA sp. ?

(Pl. 15, figs. 52–54)

LOCALITY AND HORIZON. Gebel Atshan, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

DESCRIPTION. *Fruit:* Sub-ovoid, bisymmetric about a plane which includes the two major axes and probably the funicle, although this was not actually seen, somewhat sharply angled in the plane of symmetry on one side, rounded and much inflated on the other (funicular margin). Style terminal at the apex, marked by a slight prominence. Attachment at the opposite end of the major axis to the style where the fruit shows a slight flattening, marked clearly by a small circular scar from which the surface cells radiate. The broad margin of the fruit is semicircular in outline; the narrow margin is slightly concave immediately below the style and for about one-third of the length, but is convex for the lower two-thirds. Surface puckered and wrinkled giving a leathery appearance. Surface cells obscure except around the attachment where they are equiaxial, rounded, slightly convex, and about 0·038 mm. in diameter. Length of fruit, 13 mm.; breadth in plane of symmetry, 11·5 mm.; thickness at right angles to plane of symmetry, 11 mm.

REMARKS. The solitary specimen looks like a drupe with epicarp and mesocarp preserved so that all the characters of the endocarp are hidden except so far as they can be inferred from the form and symmetry of the specimen. The peculiar asymmetric outline as viewed at right angles to the plane of symmetry and the occurrence of one broad rounded and one angled margin may indicate a fruit of Icacinaceae. But pending the discovery of further evidence the specimen can only be referred tentatively to the form-genus *Icacinicarya*.

Family FLACOURTIACEAE ?

Genus ***THIEBAUDIA*** nov.

DIAGNOSIS. A large berry with about 36 parietal placentas, numerous seeds in two close set rows on the placentas, and a pulpy mass of tissue which occupies the whole of the fruit cavity. Seeds probably sub-ovoid. Length of fruit (compressed), 13 mm.; breadth (much increased by compression but bereft of pericarp), 37 mm. Diameter of seeds, 1 to 1·5 mm.

TYPE SPECIES. *Thiebaudia rayaniensis* n. sp.

Thiebaudia rayaniensis n. sp.

(Pl. 16, figs. 58–63)

DIAGNOSIS. As for genus.

HOLOTYPE. A single fruit with most of the pericarp removed. Thiébaud & Robson Collection (Locality no. 604), 1951. Brit. Mus. (N.H.), No. V.31120.

LOCALITY AND HORIZON. Wadi Rayan, Western desert of Egypt; Eocene (? Lutetian or slightly younger).

DESCRIPTION. *Fruit:* A globular or sub-globular berry (now much compressed dorsiventrally, so that the wall has been buckled all around the equator of the specimen). Dehiscence probably by irregular breaking of the pericarp as no indication of sutures for regular dehiscence can be seen. The pericarp is preserved only at the extreme base and apex (Pl. 16, figs. 58, 59), elsewhere it has been broken away or abraded.

The external surface shows a few obscure radial flutings at the upper end, but is preserved in a matrix so coarse that it does not show the cell structure of the epicarp if still present.

A slightly defined and very slightly sunk area at the apex, about 5 mm. in diameter, may mark the base of the style. Thickness of pericarp about 3 mm. Numerous broad, rather flat, stout, longitudinal bands of fibres can be seen (although all are now incomplete) in the lower half of the fruit lying in fragmentary remains of the pericarp, but above the equator they appear to have been abraded. Placentation parietal, the seeds arranged in two close-set rows on each of thirty-six longitudinal placentas. Sometimes the seeds in the two rows are opposite one another, sometimes they appear to be alternate. Between each pair of placentas there is a very slight longitudinal ridge which thickens at its extreme apical end. These ridges produce on the inner surface of the pericarp a series of broad shallow longitudinal channels or pockets into which the placentas and seeds fitted.

Each placenta begins to produce its seeds at about 10 mm. from the apex of the fruit, where it springs from a pointed tongue of tissue with a narrow median furrow (Pl. 16, figs. 58, 60). The whole of the interior of the fruit is filled by a pulpy mass which adheres closely to the pericarp. The shallow ridges of the pericarp give rise to grooves upon the surface of the pulpy-mass. These separate the broad flat-topped ridges opposite the placentas bearing the concavities caused by the seeds.

It is the surface of this mass which is exposed intact on the upper surface of the specimen (Pl. 16, figs. 58, 60). The pulp is formed of coarsely and deeply sinuous cells, and throughout its thickness there are numerous small cavities about the same size as these cells (i.e., about 0·057 to 0·114 mm. in diameter.) No tendency to split either radially or otherwise has been detected in the pulpy mass.

Length of fruit (much reduced by dorsiventral compression), 13 mm.; breadth (correspondingly increased by compression but reduced by the loss of the pericarp), 37 mm.

Seeds: Very obscure. Producing sub-circular or sub-ovoid hollows on the pulpy mass (Pl. 16, figs. 58–61). Perhaps somewhat laterally compressed. The shallow convex external surface of the seed was ornamented with large inflated radially arranged cells or areoles diverging from a knob-like projection (Pl. 16, fig. 62). This structure is visible on the impression of a detached seed (probably belonging to the fruit) which is preserved on the pericarp near the base. Obscure traces of similar cells were also seen on a few seed-impressions on the pulpy mass. Other seed-impressions merely show a rounded prominence which must represent a considerable depression (hilar, micropylar, or chalazal ?) on the actual seed surface (Pl. 16, fig. 61, best shown in seed *s*). Internal casts of seeds (preserved in a few instances on the underside of the fruit but always incomplete, Pl. 16, fig. 63) show a smooth shining surface with longitudinal striations due to very long narrow cells with stout longitudinal walls, 0·014 to 0·018 mm. broad, lying parallel with the long axis of the seed. There are also slight traces of a coat of transversely aligned cells or fibres. Diameter of seeds, 1 to 1·5 mm. An internal cast measured 1·5 mm. in length, 1 mm. in breadth.

REMARKS. One fruit preserved in a ferruginous cement filled with quartz grains forming a hard mass. It appears to have been embedded in a cream-coloured fine sand with Nummulites. The sand filled every crack and cranny of the cast, and a Nummulite (reported by Mr. C. D. Ovey as having a range from Lutetian to Middle Oligocene) was found in sand lying in the deep hollow between the lower surface of the pulpy mass and the remains of the pericarp at its base. There can be little doubt that the Nummulite belonged to the strata in which the fruit occurred, for little attempt had been made to clean the fossil of the adherent sand which clung with persistence. It has now been boiled and the sand brushed away. Other fossils from these beds are also said to be ferruginous, but this is the only plant as yet discovered. The age of the deposit is regarded as Lutetian, or possibly somewhat younger, but definitely Eocene.

As stated, most of the pericarp of this fruit was missing, revealing the central pulpy mass. It is a difficult specimen to understand and interpret. But probably, if its living counterpart were discovered, the description given above could be considerably simplified and shortened.

The coarseness of the matrix is not well calculated to preserve fine details. Little can be seen of the seed structure, especially as the hollows on the central mass are largely merely cavities in the pulp due to the pressure exercised by the growing seeds. They do not therefore give much information apart from the size and, rather obscurely, the form of the close-set seeds which are themselves almost entirely absent. Even these impressions are partially confused by some measure of overlap. The bases of the stout fibres in the fruit wall persist in broken ragged fragments at the base of the specimen, where they project from the fragment of pericarp. Sometimes they are missing, and the openings from which they came can be seen in the edge of the broken wall. The upper side of the specimen shows in good condition the surface of the pulpy mass with impressions made by the seeds on the ridges opposite the placentas, and the shallow furrows between these ridges which are the impressions of the narrow ridges on the pericarp wall described above.

The lower surface is less well preserved. It appears to have become torn and battered before or during fossilization, so that the actual lower surface of the pulpy mass together with the alignment and ridges on this surface is largely destroyed. Traces only of these features and of the collapsed and fragmentary pericarp wall with its fibres can be detected. Detached seeds represented by occasional external impressions or true internal casts have been pushed into the soft pulp and are visible here and there. Usually the casts are obscure. The true internal casts are rarer than the external impressions.

A curious and at first misleading feature of this specimen is a coarse transversely elongate meshwork of angular ridges around the equator. A radial fracture of the pulpy mass demonstrates the purely secondary and inorganic character of these ridges, which are due to the infiltration and setting of a limonite cement in cracks caused by buckling of the walls and pulp. No organic structure is to be seen in the seams of limonite which fill these cracks.

Affinities. The parietal placentation of this multi-carpelled fruit limits relationship to very few families. At first sight the specimen recalls a Poppy capsule on account of its radial symmetry and rounded small seeds, while the remains of the fruit wall at the apex simulate the stigma-bearing disc of *Papaver*. Here, however, the resemblance ends. The pulpy mass of the interior is wholly unlike anything in Papaveraceae. Parietal placentas associated with such a mass of pulp do, however, occur in Flacourtiaceae. But the difficulty here is that in no known genus of that family do as many as 36 placentas and carpels occur, while the details of seed structure in the fossil are too imperfectly known to be conclusive. No other living family appears to bear so close a relationship to this lovely fossil, and past experience has demonstrated the tendency for a larger number of locules to occur in fossil than in living forms, although not perhaps to the degree here recorded.

In the absence of more satisfactory information the specimen has been referred doubtfully to the family Flacourtiaceae. It has been given a new generic name, *Thiebaudia*, after one of the finders, while the specific name *rayaniensis* indicates the place where it was found.

The writer is of opinion that this specimen ought to be compared very carefully with Kräusel's species *Nymphaeopsis bachmanni* from the Lower Oligocene of Cairo. The supposed placenta and unequal hammer-shaped involucral segments of that species may quite possibly be parts of a pericarp which has cracked and contracted into irregular segments on drying. Such a feature is displayed by one fruit of *Palaeowetherellia* from Kharga (Pl. 14, fig. 42), in which the cracked berry with its mineral infiltrations simulates a trifid perianth. The fibres shown by Kräusel (1939, pl. 2, figs. 2, 3, 6) on the surface exposed beneath the supposed involucral segments are not altogether unlike those of *Thiebaudia*. The direction in which they branch suggests that the supposed apex is in fact the base of the specimen. The buckling of the fruit at the equator due to dorsiventral compression has produced a similar network of infiltration ridges to those described in *Thiebaudia*. It is not impossible that the apparent operculum of the seeds might be interpreted as a large chalazal scar. But these are merely suggestions for future consideration. They cannot be substantiated without the most careful study of the specimens themselves.

Carpolithus hassani n. sp.

(Pl. 16, figs. 64, 65)

LOCALITY AND HORIZON. Gebel-el-Ter, Kharga Oasis, Egypt; Dano-Montian Lower Esna Shales.

A beautiful but puzzling specimen suggests one valve of a bisymmetric endocarp. It appears to have been rubbed down artificially at the margins but to no great depth. The outline, as it exists at present, is broadly elliptical, 20 mm. long, 17·5 mm. broad, 5·5 mm. deep. The external surface is gently convex and the internal correspondingly concave. The thickness of the wall at the polished margin is 2 to 2·5 mm.

Three deep external grooves must have some structural significance. They appear to be the outer edges of slits which pass through the whole thickness of the wall. The two nearest the margins of the valve slope inwards towards the centre of the fruit so that their inner edges, marked by deep grooves on the surface of the locule, lie slightly closer together than do their outer edges on the external surface of the valve. These two grooves are parallel with the outline of the valve, but they do not meet, although their ends lie much closer together at one extremity (apex ?) of the valve than at the other. One groove is longer than the other. The third groove which pierces the endocarp also, lies midway between the other two but is shorter than either. It begins at about the middle of the valve and passes towards that end of it (base ?), where the other two grooves are most widely separated. It dies out before reaching the edge of the valve. Within the slits the surface of the endocarp is longitudinally striate.

On the exterior, between the longer curved marginal groove and the short median one, a longitudinal slightly sinuous furrow can be seen which was evidently a channel for a fibre, impressions of which are seen. It gives off two or three short slender branches at its upper end. These diverge and taper upwards.

Surface of valve rough, due to the convex angular walls of the parenchymatous cells of which it is composed. Cells 0·05 to 0·1 mm. in diameter. Locule surface smoother, formed of equally large equiaxial cells.

A first glance at this specimen suggests that it may belong to Menispermaceae. But closer scrutiny shows that the relationship is impossible for the following reasons:

(1) The curved marginal grooves do not unite at the apex to form a horseshoe, nor does one of their opposite ends curve appreciably outwards.

(2) The external grooves correspond with internal grooves and not with internal ridges as in Menispermaceae, where the ridges form a cavity for the curved seed.

(3) The endocarp of Menispermaceae is fibrous in structure, not parenchymatous.

I have found no fruit with such peculiar slits which may be connected with germination. Possibly the curved area enclosed by the slits may be associated with a curved embryo.

Carpolithus sp. (***Icacinicarya*** sp. ?)

(Pl. 16, fig. 66)

Locality and horizon. Gebel-el-Ter, Kharga Oasis, Egypt; Dano-Montian Lower Esna Shales.

The internal cast of a valve of an endocarp 10·5 mm. long, 9·25 mm. broad, 1·8 mm. deep. The cast is formed of coarse crystalline ferruginous matter. Its surface shows an obscure network of ridges. The internal surface of the actual specimen would have shown corresponding grooves separated by shallow convexities. No cell-structure is visible. The form of the valve suggests Icacinaceae, but the evidence preserved is insufficient for certainty.

Carpolithus sp.

(Pl. 16, figs. 55–57)

Locality and horizon. Gebel Atshan, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

A sub-globular fruit slightly laterally compressed, with a three-angled apex, the angles meeting in a slight prominence. They die out at about the middle of the fruit. Between these well-marked angles a few subsidiary inconspicuous longitudinal ridges can be seen. Basal attachment small, slightly sunk, marked by a little projection at the middle of the hollow. At the extreme base of the fruit there are three short, very shallow, rounded furrows opposite the three apical ridges or angles. Surface, as now preserved, ornamented with numerous angular, more or less equiaxial contiguous concave areas, somewhat variable in size, up to 1 or 1·5 mm. in diameter but sometimes smaller. This cast is formed of radiating groups of fine cells, the groups often but not invariably coinciding with the concavities. Length of fruit, 13·5 mm.; diameter, 10 by 13·5 mm.

There is nothing to indicate the identity of this specimen.

APPENDIX I

NOTE ON THE OCCURRENCE OF THE FOSSIL FRUITS AND SEEDS COLLECTED FROM THE KHARGA OASIS, WESTERN DESERT OF EGYPT

By M. Youssef Hassan

The specimens were collected from a bed with an average thickness of 35 metres. It is composed of dark grey and greenish shales, well foliated and often densely seamed with gypsiferous and salt intercalations. Red nodules of botryoidal limonite, sometimes attaining large sizes, are abundant. Frequently the limonite appears in pseudocrystalline form, being cubes sometimes with interpenetration twinning. The bed is rich in fossils which are dwarfed and excellently preserved in limonite. The age of this bed is " Danian " or more probably Dano-Montian. The following is a complete list of the fossil fauna identified:

Schizorhabdus libycus Zittel.
Palaeopsammia multiformis Wanner.
Bathypsammia cleopatrae Hassan MS.
Trochocyathus epicharis Wanner.
Trochocyathus deniseptatus Hassan MS.
Dungulia libyca (Wanner).
Pattalophyllia aegyptiaca (Wanner).
Terebratulina sp.
Pentacrinus sp.
Nucula tremolate-striata Wanner.
Nucula chargensis Quaas.
Leda leia Wanner.
Trapezium sp.
Trapezium aff. *acutangulum* (Deshayes).
Cardium cf. *becksi* Muller.
Cardium cf. *inaequiconvexum* Cossman & Pissarro.
Crassatella zitteli Wanner.
Cucullaea schweinfurthi Quaas.
Cucullaea sp.
Limea sp.
Chlamys mayer-eymari (Newton).
Verticordia nova Hassan MS.
Corbula striatuloides Forbes.
Trochus cf. *laryi* D'Archiac & Haime.
Scala calamistrata (Wanner).
Architectonica dachelensis (Wanner).
Natica (*Gyrodes*) *farafrensis* Wanner.
Natica (*Euspira*) *terensis* Hassan MS.
Rissoa cf. *crassistriata* Wood.
Campanile cf. *brookmani* Cox.
Cerithium abictiforme Wanner.
Cerithium bigeniculatum Wanner.
Cerithium cf. *periphractum* Wanner.
" *Alaria* " *schweinfurthi* Quaas.
Cypraea cf. *kayei* Forbes.
Tonna sp.
Tudicla peroni Quaas.
Sassia tuberculosa (Kaunnowen).
Sassia farafrensis (Quass).
Sassia chalmasi (Quaas).
Sassia sp.
Athleta (*Volutilithes*) *daniensis* (Quaas).
Cyclichna cf. *regulbiensis* (Adams).
Solidula chargensis (Quaas).
Solidula pharaonum (Wanner).
Avellana cretacea Quaas.
Pyrgopolon sp.
Nautilus applanatus Wanner, *ex* Zittel MS.
Nautilus desertorum Quaas, *ex* Zittel MS.

This horizon is resting on a series of alternating marls and impure limestones with occasional phosphatic bands of undoubtedly late Maestrichtian age.

APPENDIX II

NOTE ON THE OCCURRENCE OF THE FOSSIL FRUITS AND SEEDS COLLECTED FROM THE KOSSEIR AREA (RED SEA), EGYPT

By Murad I. Youssef

The fruits were collected from a single bed in different localities in the Kosseir Area (Red Sea). The bed in which these fossil fruits, as well as the fossils mentioned below, were found is a greyish-green shale varying in thickness between 50 and 125 metres. The concretions found throughout this bed, and the fossils occurring generally in a band near its middle part, are all limonitic. Cubic pseudomorphs of limonite, probably after pyrite, are also found. Irregular gypsum veins running in every direction, perhaps corresponding to the more or less pyramidal planes of jointing of the shales, are epigenetic, being secondary in origin.

The fossils collected from this bed are considered to be Danian or Dano-Montian. Some 30 metres of shales and marls lying immediately below this bed are of the same age. These are underlain by Maestrichtian rocks containing many phosphate and phosphatic beds.

The following is a list of the fossil fauna identified from the thick shale bed :

Brachycyathus daniensis Wanner.
Trochocyathus epicharis Wanner.
Pattalophyllia aegyptiaca (Wanner).
Caryosmilia granosa Wanner.
Dungulia milneri (Gregory).
Dungulia libyca (Wanner).
Caryophyllia jasmundi Wanner.
Palaeopsammia multiformis Wanner.
Stephanophyllia (*Microbacia*) sp.
Serpula cf. *discoidea* Wanner.
Pentacrinus sp.
Salenia sp.
Cyphosoma sp.
Hemiaster chargensis Wanner.
Hemiaster (*Leucaster*) *lamberti* Cottreau.
Terebratulina chrysalis (Schlotheim).
Terebratulina sp.
Nucula chargensis Quaas.
Nucula lucida J. Boehm.
Nucula tenera J. Müller (*non* S. V. Wood).
Nucula tremolate-striata Wanner.
Leda leia Wanner.
Thyasira cretacea (Wanner).
Cardium cf. *inaequiconvexum* Cossmann & Pissarro.
Cardium cf. *becksi* Müller.
Trapezium sp.
Lucina dachelensis Wanner.
Crassatella matercula Mayer-Eymar.
Arca modioloides Wanner.
Cucullaea sp.
Chlamys mayer-eymari (Newton).
Verticordia nova Hassan MS.
Scala cf. *desertorum* Wanner.
Natica farafrensis Wanner.
Campanile cf. *brookmani* Cox.
Alaria schweinfurthi Quaas.
Alaria sp.
Sassia chalmasi (Quas).
Neptunea zitteli (Quaas).
Neptunea sp.
Fusus sp.
Athleta (*Volutilithes*) *desertorum* (Quaas).
Solidula chargensis (Quaas).
Avellana cretacea Quaas.
Avellana sp.
Cylichna cf. *regulbiensis* (Adams).
Dentalium bicarinatum Wanner.
Nautilus desertorum Quaas, *ex* Zittel MS.

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NOTE.—While this paper was going through the press my attention was drawn to a memoir by L. W. LeRoy (Biostratigraphy of the Maqfi Section, Egypt. *Mem. Geol. Soc. Amer.*, Washington, **54**, 1953) in which, from a study of the Foraminifera, the author concludes not only that the "Esna Shales" are definitely Lower Eocene, but also that the Danian is probably unrepresented in Egypt. There may, however, be some unresolved confusion over the use of the term "Lower Esna Shales."

PLATE 10

Nipa burtini (Brongniart)

Fig. 1. The domed apical end of a drupe which is incomplete below the middle. Length preserved, 25 mm.; breadth, 27 mm. Estimated complete length, about 45–50 mm. It shows the typical longitudinal fibro-vascular bundles embedded in parenchyma. (*u*) the apical umbo. × 2·8. (V.31105.)

Fig. 2. The same, viewed from below, looking on to the fractured surface. The side shown in fig. 1 is towards the top of the figure. Part of the unridged smooth endocarp (*e*) is exposed. Transverse fibres of the endocarp are obscurely seen. The pericarp is in section at (*p*, *p*) and in surface view with its longitudinal fibres at (*f*). × 2·8.

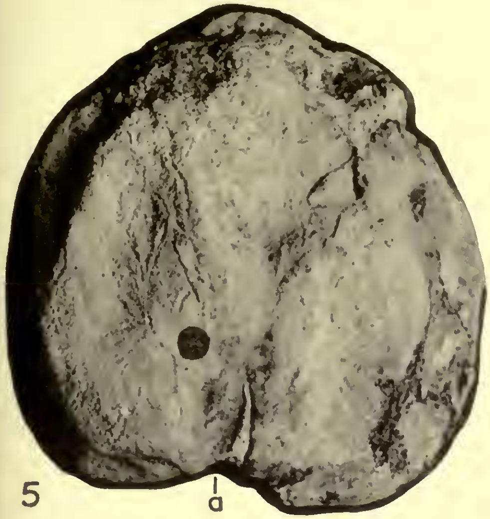
Fig. 3. An obliquely distorted seed-cast in which the basal aperture (*a*) occupies a basi-lateral position. Slight longitudinal flutings of the surface are visible. There is a mosaic pattern all over the surface. × ½ approx. (V.13239.)

Fig. 4. The opposite surface of the same seed-cast, apical end, showing the sub-apical funnel-shaped opening (*ch*) and the raphe-fibre impressions converging towards it and passing into it. (*m*) marks the apical mucro of the nut. × 1·2.

Fig. 5. A seed-cast so compressed as to be almost lenticular. (*a*) is the position of the basal aperture. The coarse network of fibres which lay between the two integuments of the testa is faintly impressed upon the cast to the left of the median line. × ½ approx. (V.13240.)

Nipa fruticans Thunberg

Fig. 6. A seed for comparison with fig. 5 from which the outer coat of the testa has been entirely removed. Most of the inner coat has also been removed except beneath the slightly sunk coarse network of fibres (*f*, *f*) which lay between the two coats and which still adheres to the seed. In the meshes between the fibres (where the inner coat has gone) the transverse alignment of the small ruminations of the endosperm can be seen rather obscurely. The seed has been cut longitudinally. × 2 approx. Recent; Singapore.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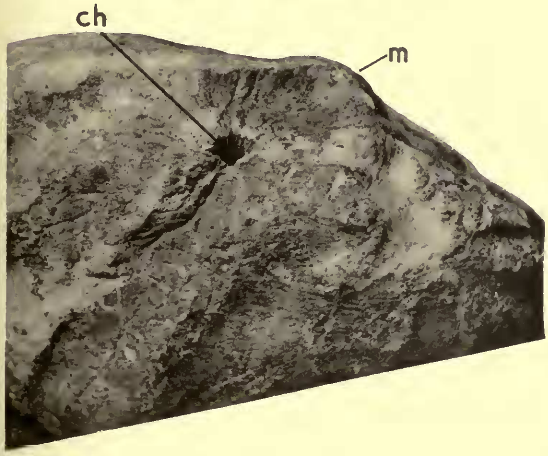
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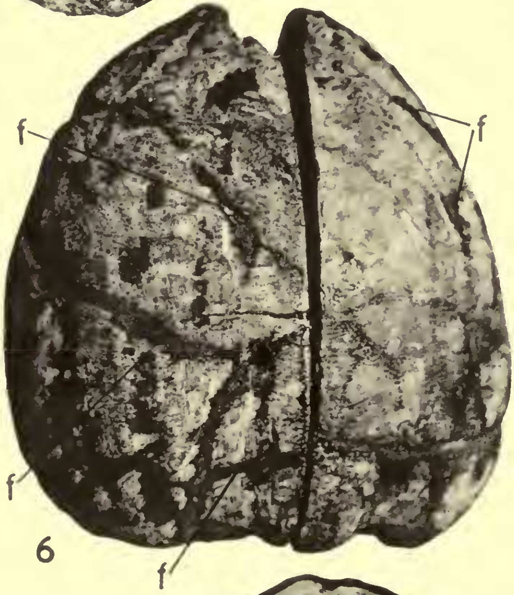
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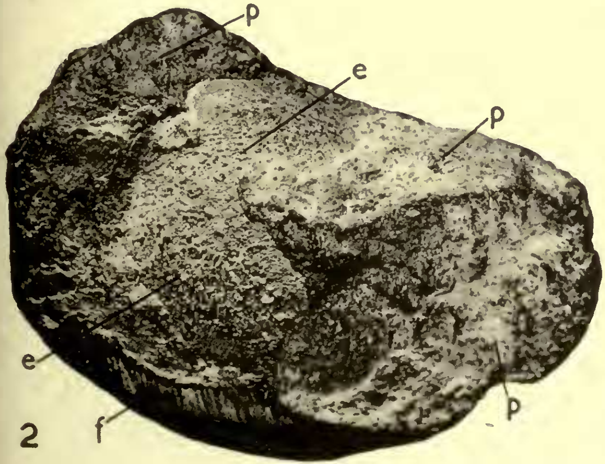
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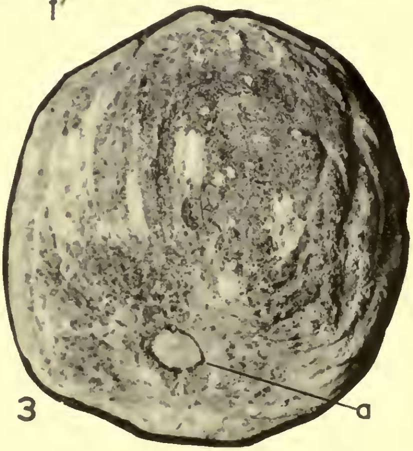
3

NIPA BURTINI, NIPA FRUTICANS

PLATE 11

Nipa burtini (Brongniart)

FIG. 7. Opposite side of the seed-cast in Pl. 10, fig. 5, showing detail of endosperm structure. The elongate alignment at (*r*) indicates the position of the raphe, the radial arrangement indicates the point of entry of the raphe fibres (*ch*) below the apex of the cast. × 1·8.

FIG. 8 The same seed-cast, detail of the surface depicted in Pl. 10, fig. 5, showing the more normal transverse alignment of the endosperm. × 1·8.

FIG. 9. The base of a seed with its ribbed outer integument partially preserved but sufficiently abraded to expose the flat broad fibre band (*f*). The basal aperture is clearly seen. The specimen has undergone much lateral compression. × 1. Figured by Kräusel, 1939, pl. 1, fig. 24 as *Rubiaceocarpum markgrafi*.

Nipa fruticans Thunberg

FIG. 10. A seed, side, showing the ribbed outer integument with clear impressions of the longitudinal, and more obscure impressions of the transverse, endocarp fibres. × 1·7. Recent; Singapore.

FIG. 11. The seed in Pl. 10, fig. 6, showing the flat raphe band (*r*) lying in a shallow longitudinal furrow of the endosperm. On each side of the band the transverse alignment of the endosperm is visible. Above where the band has been removed irregular arrangement of the endosperm is exposed at (*ch*) and just below longitudinal alignment can be detected. × 2 approx.

FIG. 12. The same seed, base, showing the aperture for the radicle, the deep furrow (*g*) due to the incomplete septum which projected from the locule-wall, and shallow furrows or sinuosities of the surface. The raphe lay in the furrow at (*r*). × 1·75.

Anonaspermum aegypticum n. sp.

FIG. 13. The distal end of a seed-cast showing typical ruminate endosperm with encircling raphe seen at (*r*, *r*). The fibrous remains of testa still adhere in the depression at the middle of the broad surface. The specimen had been fractured transversely and the hilar end was missing. (*ch*) indicates the beginning of the chalaza, most of which has been broken away with the hilar end. × 3. (V.31106.)

FIG. 14. The same, end view. It shows the encircling raphe partly broken on the left so that the ruminations are exposed in section at *rs*. The chalaza begins at (*ch*). × 3.

FIG. 15. The same, fractured surface, showing the four-partite endosperm. × 3.

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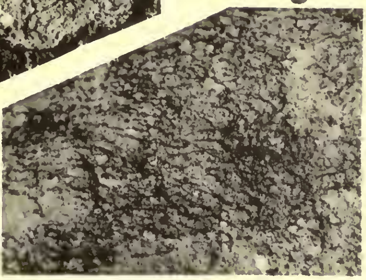

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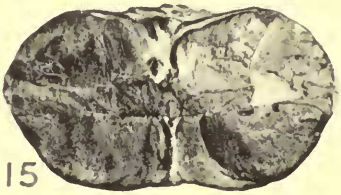

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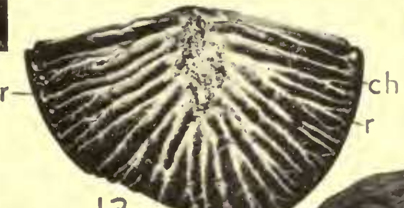

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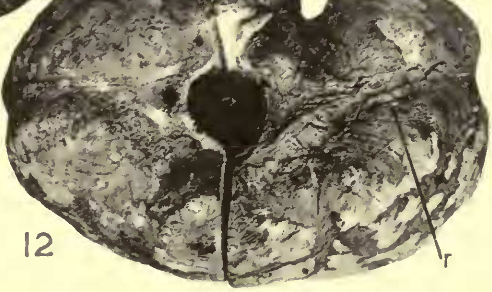

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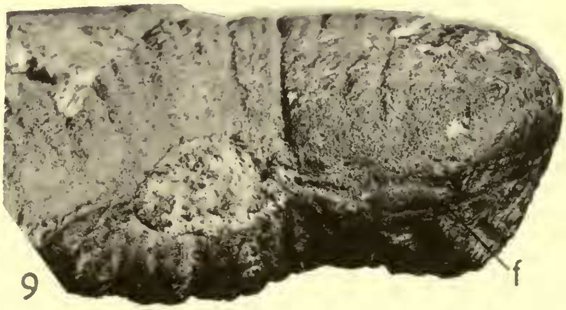

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NIPA BURTINI, NIPA FRUTICANS, ANONASPERMUM AEGYPTICUM

Lagenoidea trilocularis Reid & Chandler

FIG. 16. Side view of a fruit showing three of the six loculicidal segments of the capsule. × 3. (V.31107.)

FIG. 17. Base of the same specimen, showing the attachment scar and wrinkled epicarp which partially obscures the segments. × 3.

FIG. 18. Apex of the same, showing more clearly the six segments and lines of dehiscence. × 3.

FIG. 19. Side view of a second specimen showing three segments clearly; the edge of a fourth is just visible on the right-hand margin of the figure. × 2·8. (V.31108.)

FIG. 20. The same, base, showing six segments and an aperture where placenta and perianth have broken away. × 2·6.

Lagenoidea bilocularis Reid & Chandler

FIG. 21. A fruit, side, showing the narrow median segment representing the edge of the septum, and two of the broader lateral segments. × 3. (V.31109.)

FIG. 22. The same, apex, showing the narrow median segments which form the ends of the septum and the two pairs of segments which overlie the locules. Loculicidal splitting occurs at (*l*, *l*), septicidal splitting at (*s*, *s*). × 3.

FIG. 23. The same, base. The septum is damaged on one side at this end of the fruit. Lettering as in fig. 22. × 3.

Palaeowetherellia schweinfurthi (Heer) Chandler

FIG. 24. Lower surface of a six-carpelled endocarp showing the six loculicidal suture lines (*l*, *l*). Slight abrasion of this surface has displayed the radiating groups of fine parenchyma which produce a pitted effect. Decay at the centre of the base has scarcely started. × 2·8. (V.31110.)

FIG. 25. The same, apex. The outer part of the carpel wall is corroded in places showing the finer-celled parenchyma of the layers beneath. Loculicidal sutures are clear; the septicidal ones (*sp*, *sp*) between them are more obscure except where abrasion has partly removed the outer layers of the endocarp. × 2·8.

FIG. 26. The under surface of an eight-loculed endocarp, perfect except for the characteristic decay at the centre of the base so that locules and septa (showing planes of weakness associated with septicidal splitting) are exposed. Several locules have shed their seeds. In others the seeds are ill-developed. × 2·8. (V.31111.)

FIG. 27. The base of half a fruit which retains a considerable patch of exocarp (*ex*) over the median area. Around the circumference the exocarp has been worn away exposing six segments of endocarp representing seven locules (*l*, *l*). × 2·8. (V.31112.)

FIG. 28. The fractured surface of the same showing two locules. The one on the right is occupied by a locule- and seed-cast. (*ch*) indicates the position of the chalaza. The left-hand locule is empty but the much encrusted funicle (*f*) is visible. Its origin in the axis is obscured by mineral deposit. (*ex*) = exocarp in section. × 3.

FIG. 29. Base of another incomplete endocarp with three and a half segments representing four locules (*l*, *l*). The half segment on the right has slipped out of position along the loculicidal fracture plane (*l*). The surface of this half segment shows the plane of septicidal fracture (*sp*). × 2·8. (V.31113.)

FIG. 30. The same, looking on to the fractured surface. (*sp*) is the septicidal fracture plane. (*l*, *l*) indicates loculicidal surfaces. The network of fibres is seen on the right-hand loculicidal suture surface. The left locule surface is obscured by molluscan casts (out of focus in the figure). × 3.


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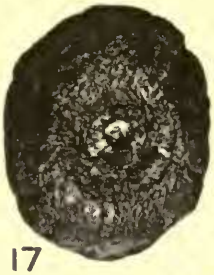
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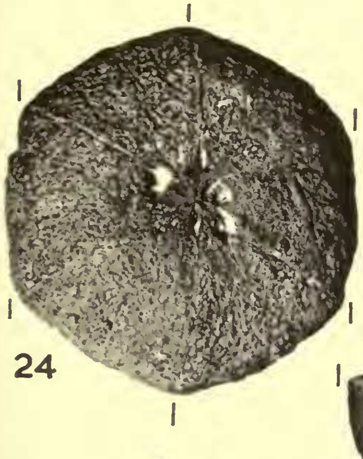

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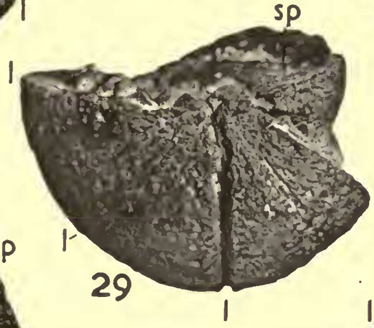

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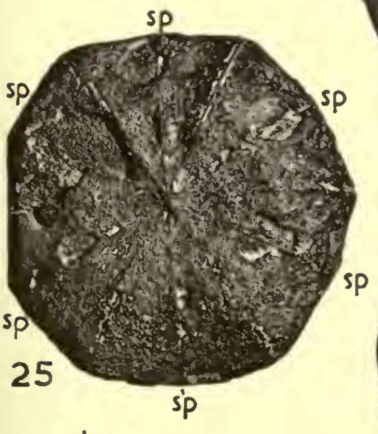

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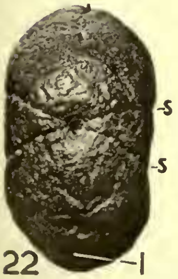

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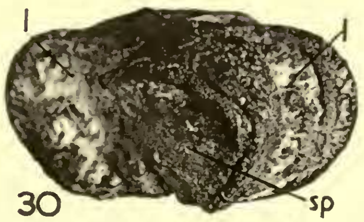

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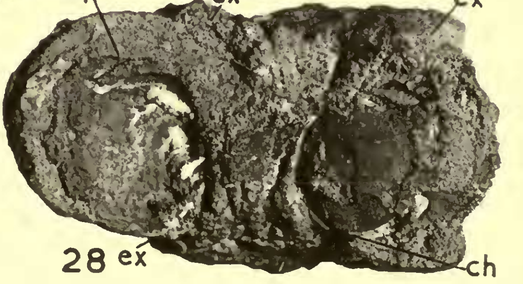

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LAGENOIDEA TRILOCULARIS, L. BILOCULARIS,
PALAEOWETHERELLIA SCHWEINFURTHI

PLATE 13

Palaeowetherellia schweinfurthi (Heer) Chandler

FIG. 31. The apex of a nine-carpelled fruit polished by abrasion. (*l*, *l*) indicates planes of loculicidal dehiscence. Between them, but more obscure, are radial lines indicating planes of septicidal dehiscence (*sp*). At (*ls*) incipient loculicidal splitting can be seen at the middle of the ridge. The specimen has been fractured along the line (*f*, *f*). The small circular scar at the centre may be the axis or the style base. × 3. (V.12985.)

FIG. 32. The same, base, corroded at the centre so that the locules are exposed (some now empty). Note the conspicuous pits over the surface due to the decay of fibres surrounded by coarse parenchymatous patches. Lettering as in fig. 31. × 3.

FIG. 33. The fractured surface (longitudinal section) of the above showing a locule-cast on the left with the funicle arising from the axis of the fruit and passing in the plane of the locule to the hilum situated near the upper outer angle. The right-hand locule is empty. × 3.

FIG. 34. The counterpart half of the same, showing on the right the locule surface which overlay the cast in fig. 33, and on the left an abortive locule-cast which occupied the empty locule in fig. 33. × 3.

FIG. 35. The left-hand part of the section in fig. 33. A larger magnification shows the funicle just above the locule-cast and the entry of the funicle into the cast marking the position of the hilum on the enclosed seed. This fertile locule lies at (*fl*) on the left of fig. 32 where the edge of the cast is seen. Around the hilar end of the cast adherent patches of tissue torn from the endocarp simulate a rugose testa. × 7.

FIG. 36. The left-hand part of the section in fig. 34. The fibres of the axis show more clearly. Oblique fine striations on the surface of the abortive locule close to the axis are visible and the small abortive locule-cast is shown at (*a*). This locule lies at (*fl*) on the left of fig. 31. × 7.

FIG. 37. The same as fig. 34, right-hand side of specimen, with a detached seed from another specimen laid in the locule to show the approximate position that the seed would have occupied. Axial fibres (*a*) and funicle (*f*) are well shown in the endocarp wall and on the flat surface of the locule respectively. The curved line at the rounded end of the seed is an accidental fracture. × 7. (cf. Pl. 14, figs. 43–47.)

FIG. 38. A segment of another fruit which has broken loculicidally, apex. Axis to left at (*a*), circumference to right, loculicidal surfaces above and below. × 6. (V. 31114.)


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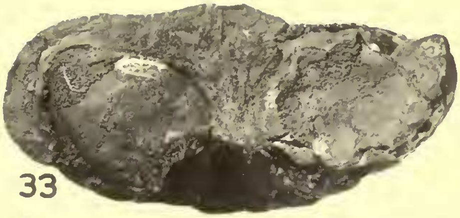
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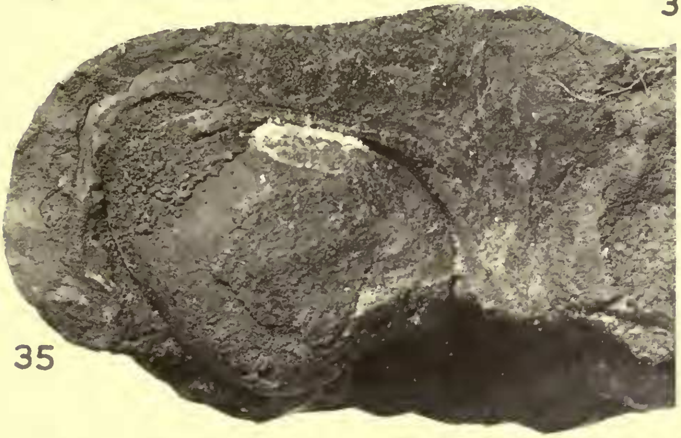
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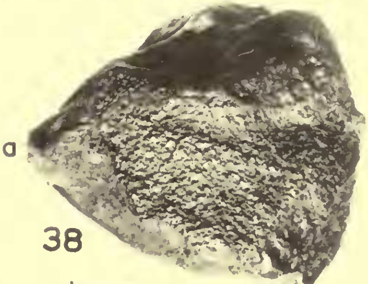
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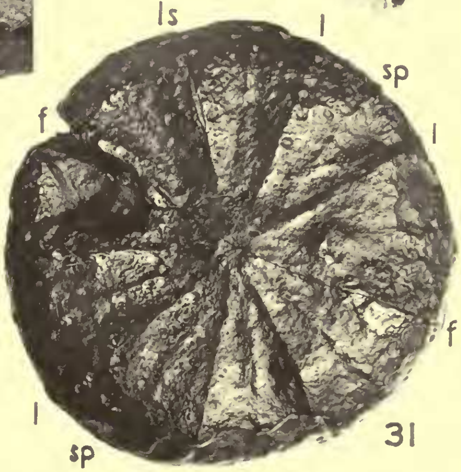
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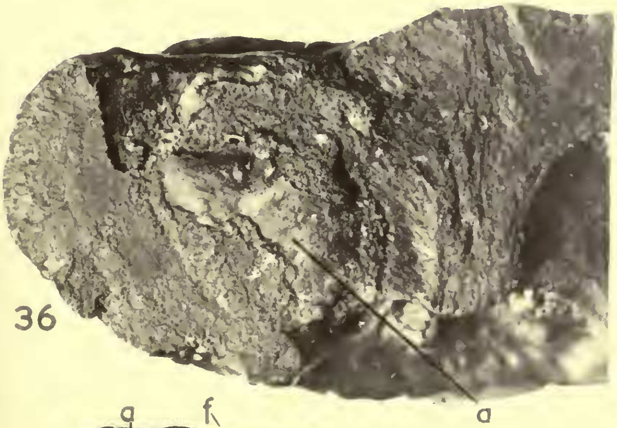
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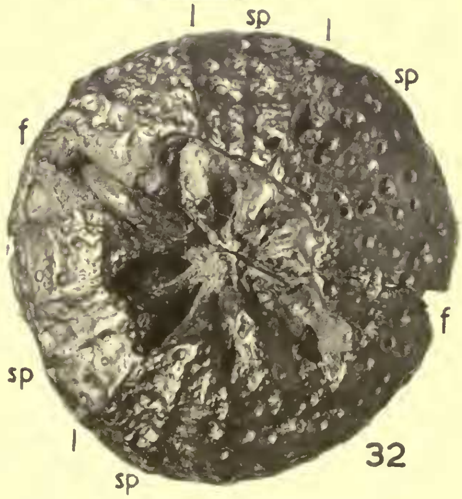
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PALAEOWETHERELLIA SCHWEINFURTHI

PLATE 14

Palaeowetherellia schweinfurthi (Heer) Chandler

FIG. 39. Side view of the fruit segment in Pl. 13, fig. 38. It shows the rounded inner end of a seed-cast (*c*) exposed by the breaking away in fossilization of the axis and inner angle of the carpel. Specimens with similar proportions were separated by Heer (1876) under the name *Royena desertorum*. × 6.

FIG. 40. The same, looking on to the inner edge where the two locules and seed-casts can be seen. × 6.

FIG. 41. Opposite side of the segment to that shown in Fig. 39. Part of the carpel wall still adheres to the cast at the outer end ; it conceals the hilar end of the seed and embracing locule-cast, and produces the false effect of a rough nodular testa. The smooth surface at (*lc*) is the remains of the thin locule-cast closely adherent to the seed. To the left at (*sc*) the film of locule-cast has broken away, exposing the seed-cast. A narrow band of the smoothly finished loculicidal surface is preserved at (*ls*), but elsewhere this surface has been torn away, thereby exposing the angular cells of the carpel wall at (*cw*). × 10.

FIG. 42. Apex of another fruit (incomplete as indicated by dotted lines) with exocarp preserved. Crushing and drying have caused the specimen to crack, white calcite has been deposited in the cracks which give a false appearance of three perianth segments. The specimen had been rubbed down along a plane parallel with its axis at (*p*). × 1·8. (V.31115.)

FIG. 43. The same, base. A crack on the right exposes a shining seed-cast. This cast is illustrated laid in the locule of another fruit in Pl. 13, fig. 37. Calcite-filled cracks are again seen. Lettering as in fig. 42. × 1·8.

FIG. 44. Part of the same, more highly magnified and tilted to show the seed-cast of which the lower margin is exposed. × 6.

FIG. 45. The same seed-cast, removed from the fruit, showing the narrow ventral edge. The micropyle is at (*m*), the hilum at (*h*). The plasticene in which it was necessary to mount the specimen to obtain this view of the seed somewhat obscures its outline at the lower end of the figure. × 6·5.

FIG. 46. The same seed-cast, side view. (*m*) indicates the position of micropyle and radicle, (*h*) that of the hilum. The chalaza lay near the lower end of the accidental fracture line. × 10.

FIG. 47. The same cast, opposite surface, to show the bisymmetry of the seed. × 10.

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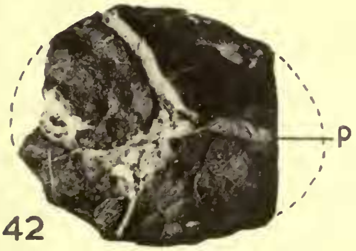

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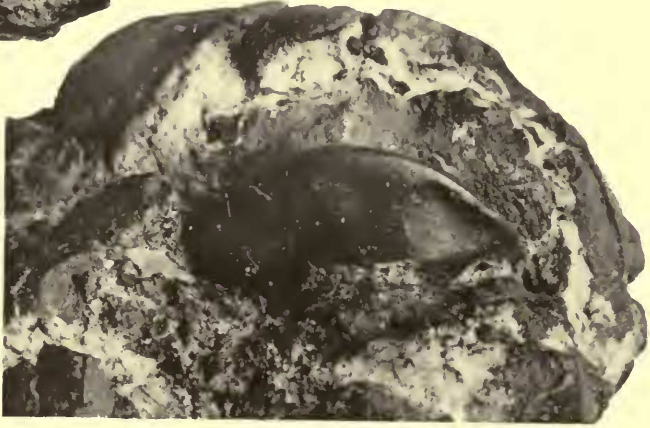

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PALAEOWETHERELLIA SCHWEINFURTHI

PLATE 15

Palaeowetherellia schweinfurthi (Heer) Chandler

FIG. 48. The partially polished surface (*p*) of the fruit in Pl. 12, figs. 41, 42, showing a tangential section through a locule and seed. The seed-cast (*sc*) is closely embraced by the locule-cast (*lc*) lying between the two thick loculicidal valves of the carpel. The raphe (*r*) is probably indicated by the slightly constricted area at the narrow upper edge of the seed-cast. The white mass to the right is calcite filling the loculicidal split and now cementing together the two valves of the carpel (*v*, *v*). × 10.

Icacinicarya youssefi n. sp.

FIG. 49. A fruit, broad surface, showing form and ornamentation. (*st*) indicates the position of the style. The funicle was situated in the right margin of the enclosed endocarp. × 2·6. (V.31116.)

FIG. 50. The same, opposite surface. Contraction of the pericarp has brought out the outline of the endocarp within. × 2·6.

FIG. 51. An endocarp bereft of the pericarp. Note the surface ornamentation, the basal aperture for the entry of the funicle at (*f*), and the short vertical fracture with infiltrated mineral substance at the stylar end (*st*). × 2·6. (V.31117).

Icacinicarya sp. ?

FIG. 52. Side view of a wrinkled drupe showing the asymmetry characteristic of Icacinaceae. The more convex left margin may be presumed to carry the funicle. (*st*) indicates the style. × 2·8. (V.31118.)

FIG. 53. Base of the same, showing the inflated funicular margin (below) and narrow opposite margin (at the top of the figure). The small circular scar of attachment, from which the cells radiate, is seen at the centre. × 3.

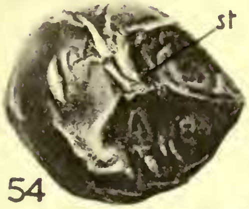
FIG. 54. Apex of the same. Funicle bearing margin to the left. Style at (*st*). × 2·6.

Carpolithus sp.

FIG. 55. Fruit, side, showing an angle at the apical end and small angular concavities all over the surface. × 2·8. (V.31119.)

FIG. 56. The same, apex, showing the three angles or ridges and the surface concavities. × 2·6.

FIG. 57. The same, base, showing the slightly sunk attachment and the surface concavities, as well as the shallow grooves which lie opposite the apical angles. × 3.



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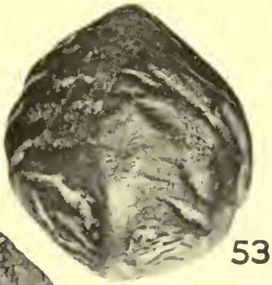

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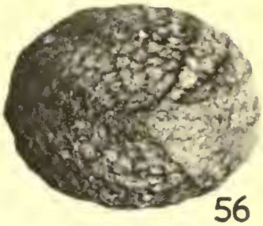

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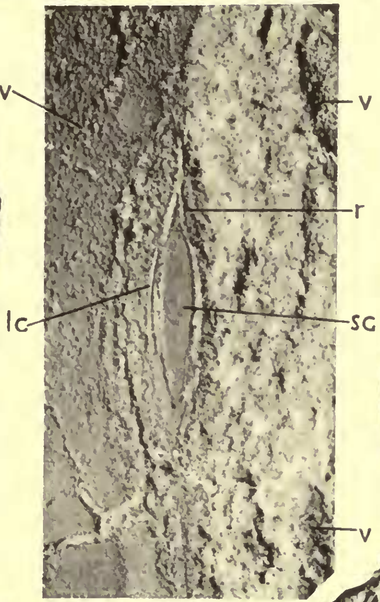

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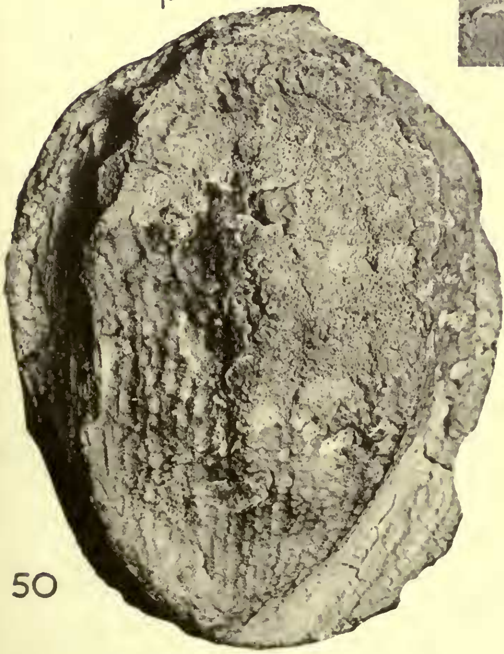

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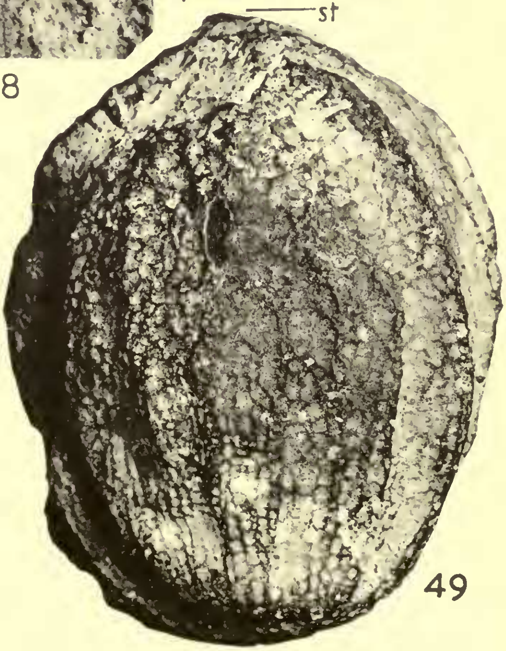

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PALAEOWETHERELLIA SCHWEINFURTHI, ICACINICARYA YOUSSEFI, ICACINICARYA SP. ? CARPOLITHUS SP.

PLATE 16

Thiebaudia rayaniensis n. gen. et sp.

FIG. 58. Apex of fruit. The pericarp is preserved only at the centre. It shows shallow, inconspicuous, radial furrows diverging from a slightly sunk circular area (perhaps the style base). Where the pericarp is broken away, the pulpy mass which fills the fruit cavity is exposed. On the surface of this mass radial furrows mark the position of shallow longitudinal ridges which must have projected from the fruit-wall. Between them impressions of the placentae are seen each with two rows of seeds now represented by the hollows which they produced on the surface of the pulp. Each placenta arises from a short tongue of tissue with longitudinal median furrow. These tongues project from beneath the edge of the remaining pericarp. × 1·6. (V.31120.)

FIG. 59. The same, from below. Here the pericarp is preserved only at the very centre of the base. The radial furrows (so clear on the upper surface) are obscure, for this surface has been much battered and partially destroyed. The arrangement of the seeds has been disturbed, but a few external seed impressions and internal casts are preserved scattered somewhat irregularly. A small concavity, seen at the lower edge of the central fragment of the pericarp, may be the external impression of a detached seed (cf. fig. 62). × 1·6.

FIG. 60. Part of the upper surface (indicated by (*x*) in fig. 58). It shows more clearly the seed pockets on each side of the placentas, and the impressions of the ridges described above. The margin of the fragment of pericarp lies near the base of the figure at (*p*). × 6.

FIG. 61. Part of the under surface (indicated by (*x*) in fig. 59) showing a few of the hollow pockets for the seeds. They sometimes show a central projection (best seen in the hollow marked *s*) which suggests a concavity on the surface of the seed. A few broken fibre-fragments (remains of pericarp) adhere to the pulpy mass. × 6.

FIG. 62. The external impression of the seed (?) on the pericarp in fig. 59 as described above. The surface of the pericarp was painted white around the impression to bring out its outline. A central depression must correspond with a prominence on the seed itself. Coarse cells or areoles are obscurely seen diverging from this central depression. × 16.

FIG. 63. A somewhat imperfect internal cast of a seed from the lower surface of the pulpy mass. Striae due to cells on the surface of the cast lie parallel with its longer axis. Although the cast is obscure a sharp marginal angle suggests a bisymmetric form. × 20. (V.31120.)

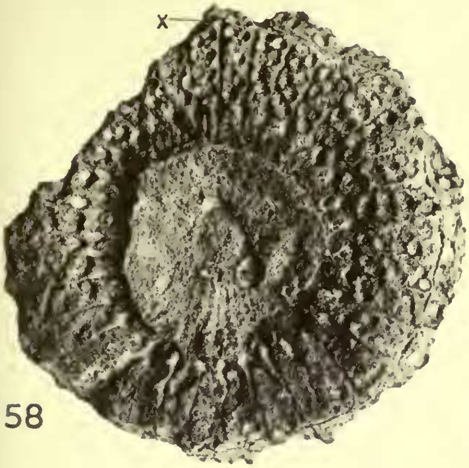
Carpolithus hassani n. sp.

FIG. 64. The exterior of a valve showing three deep furrows and a branching fibre which is partially embedded in the surface between the right-hand furrow and the short middle one. × 1·8. (V.31121.)

FIG. 65. The internal aspect of the same, showing that the wall is pierced by the three external furrows. The thickness of the wall is also shown. The smooth marginal areas appear to have been artificially produced by polishing. × 1·8.

Carpolithus sp. (*Icacinicarya* sp. ?)

FIG. 66. The internal cast of a valve of a fruit showing form and ornamentation suggestive of Icacinaceae. × 1·8. (V.31122.)



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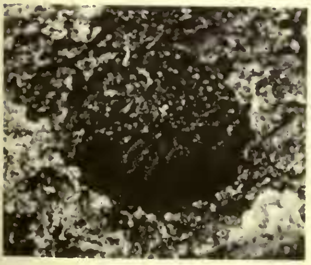

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THIEBAUDIA RAYANIENSIS, CARPOLITHUS HASSANI
CARPOLITHUS SP. (ICACINICARYA SP.?)